CONTRIBUTIONS IN MARINE SCIENCE

VOLUME 20 | SEPTEMBER 1976

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VOLUME 20 SEPTEMBER 1976

PUBLISHED BY

THE PORT ARANSAS MARINE LABORATORY

UNIVERSITY OF TEXAS MARINE SCIENCE INSTITUTE

PORT ARANSAS, TEXAS

Founded by E. J. Lund in 1945

Editor: Donald E. Wohlschlag
Editorial Assistant: Ruth Grundy

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Contents

Instructions to Authors iii

Circulation and Salinity Distribution in Coastal Louisiana Bayous. *Björn Kjerfve* 1

Periodic Phenomena at the Mouth of the Mississippi River. *Wm. J. Wiseman, Jr., L. D. Wright, L. J. Rouse* and *J. M. Coleman* 11

Seasonality and Physico-Chemical Ranges of Benthic Macrophytes from a North Florida Estuary (Apalachee Bay). *Michael S. Zimmerman* and *Robert J. Livingston* 33

Geographic Variations in Salt Marsh Macrophyte Production: A Review. *R. E. Turner* 47

Stress and Community Structure of Macrobenthos in a Gulf Coast Riverine Estuary. *Richard C. Harrel, Jimmy Aschraft, Randall Howard* and *Larry Patterson* 69

Western Gulf of Mexico Records of *Stenoninereis martini* Wesenberg-Lund 1958 (Polychaeta, nereidae) with Contributions to its Habitat Ecology. *Grady E. Williams III, Mark J. Poff* and *James T. McBee* 83

A Survey of Gammarid Amphipods of the Barataria Bay, Louisiana Region. *James D. Thomas* 87

Calaniod Copepods of the Genus *Euchirella* from the Gulf of Mexico. *Taisoo Park* 101

Tidal and Diurnal Rhythms of Locomotory Activity and Oxygen Consumption in the Pink Shrimp, *Penaeus duorarum. C. B. Subrahmanyam* 123

Seasonal Patterns in the Respiratory Metabolism of the Mullets *Mugil cephalus* and *Mugil curema. Richard H. Moore* 133

CIRCULATION AND SALINITY DISTRIBUTION IN COASTAL LOUISIANA BAYOUS*

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ABSTRACT

Time-averaged discharge and salinity distribution in a number of shallow, interconnected bayous in the Barataria basin of coastal Louisiana were determined for a 7-day period in June 1971. Measurements of current velocity, electrical conductivity, and water temperature were made at 25 stations, with continuous tide and wind records from one location. Sampling was systematic with replications on six stages of the diurnal tidal cycle and with compensation for the fortnightly tidal period. A technique is developed to compute the time-averaged discharge at each station from one vertical velocity profile per stage. From this data, the bayou system may be classified as a type 1a estuary (Hansen and Rattray, 1967). Effective horizontal diffusion accounts for the upstream salt transport in the absence of gravitational circulation and is on the order of 10^3 m^2 s^{-1}, indicating the importance of wind-induced as well as tidal mixing in the shallow lakes.

INTRODUCTION

The interdisciplinary Sea Grant program in Louisiana has primarily been focused on a small salt marsh system surrounding Airplane Lake on the western edge of Caminada Bay, 40 km west of the Mississippi River delta (Fig. 1). Emphasis has been placed on biological and geochemical marine science and numerical modelling. As hydrographic measurements have largely been neglected, this study was undertaken to determine the circulation and salt distribution of the Airplane Lake estuarine bayou system, and to calibrate numerical flow models. The major objective is to present and interpret data of direct use to marine researchers in the area. In addition, it is desirable to relate the novel study design and analysis technique, as these could successfully be applied to other systems. This study is also a good example of how a hydrographic investigation simply can be carried out on an extremely low budget.

SAMPLING DESIGN

Measurements were made at 25 stations (Fig. 1), selected in such a way that flow continuity could be established between the stations. To simplify the analysis, all readings were made in the

* Contribution No. 133 from the Belle W. Baruch Institute for Marine Biology and Coastal Research.

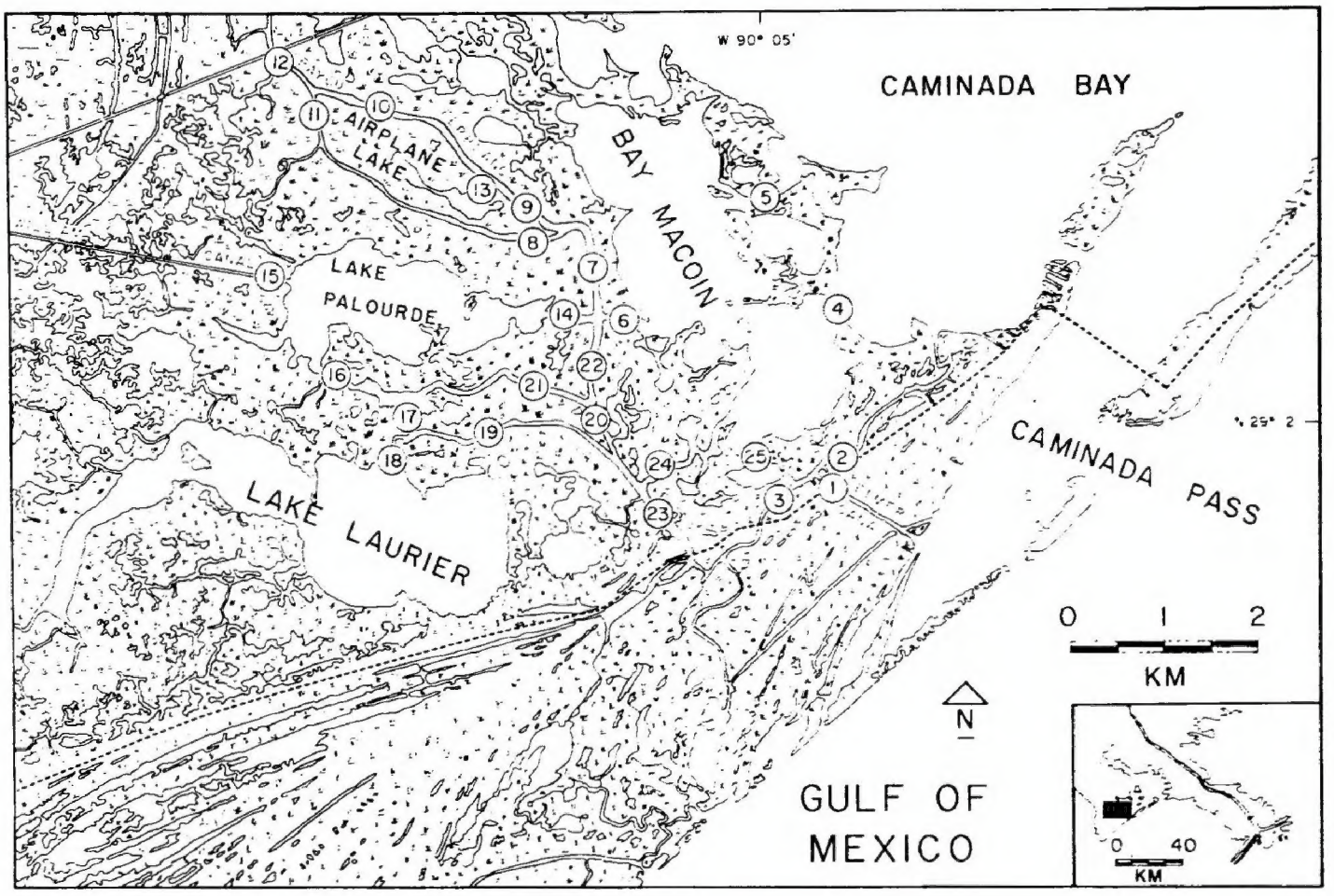

FIG. 1. Area map indicating station locations.

middle of bayous or restricted passages, thereby minimizing secondary flow, i.e. all currents were considersed to be parallel to bayou levees.

The tide in the Gulf of Mexico is primarily diurnal with a pronounced fortnightly cycle. Although the mean range at Caminada Pass is no more than 27 cm (National Ocean Survey, 1974), current velocities and salinities were known *à priori* to vary largely with the tide. Therefore, each tidal cycle was subdivided into six stages (Fig. 2). Stage 1 was chosen to begin at high water and stage 3 to end at low water. The three stages during each falling tide were taken to last equally long. Similarly, stage 4 was chosen to begin at low water and stage 6 to end at high water, the duration of the three rising tide stages being equally long for a particular tide cycle.

Sampling was based on predicted times of high and low water at Caminada Pass in an attempt to visit each station at least once per stage. However, subsequent to the study, when the Airplane Lake tide record (Fig. 2) was analyzed, it was necessary to reallocate some measurements from predicted to actual stages. In a few instances, this resulted in missing data for some stations and stages, while other stations were covered several times during a particular stage. Some tidal phase differences probably occurred within the study area but were judged to be insignificant as 1) the stations were located closely together, and 2) the actual tide at station 13 lagged the predicted Caminada Pass tide by an average of no more than 65 min or less than 5% of a tidal cycle.

The sampling design is analogous to a randomized block design in which stations are the treatments with replications taking place over the tidal stages (Snedecor and Cochran 1967). Sampling was performed in a randomized manner with respect to time within each stage at each station.

The 7-day study took place June 21–28, 1971, so that sampling began 3.5 days after the occurrence of a tropic tide and ended 3.5 days prior to the following equatorial tide. Thus, the results may be taken to represent typical conditions over the fortnightly cycle for this time of year, without bias toward high or low tide range. It should be emphasized that this is a valid approach only since the actual difference in range between the tropic and equatorial tides during this fortnightly cycle was relatively minor.

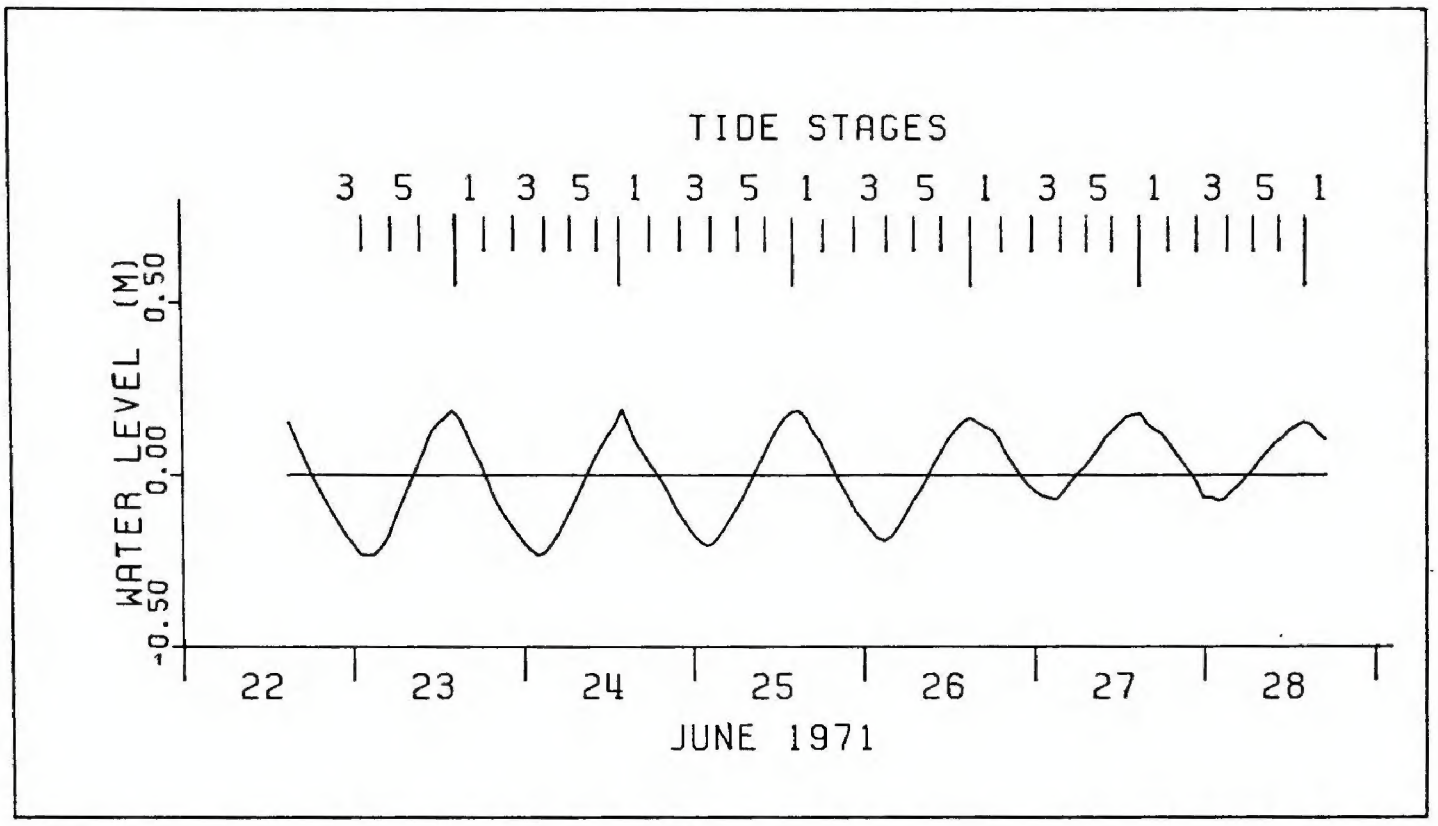

FIG. 2. Tide record measured at the entrance to Airplane Lake, station 13. The actual duration of the tide stages is also shown.

MEASUREMENTS AND ANALYSIS

Measurements of current velocity, electrical conductivity, and water temperature were made at the 25 stations at meter (occasionally half-meter) intervals from the surface to the bottom. The study, which covered day and night conditions, resulted in 172 vertical profiles of each of these parameters (Kjerfve 1972).

Biplane current crosses (Pritchard and Burt 1951, Foerster 1968) were used to measure current velocities. The crosses were made of polyvinyl chloride sheets, were calibrated statistically, and have an estimated precision of ± 1 cm s^{-1} (Kjerfve 1972). The instantaneous velocity profiles were plotted and the depth-averaged values, $\overline{V(t)}$, were calculated for each profile for later use in the computation of discharge. The maximum measured velocity was 95 cm s^{-1} (station 1, stage 5, 1 m below the surface), however, typical velocities at the 25 stations varied between $\pm$ 45 cm s^{-1}.

Conductivity and temperature measurements were made with a Martek Water Quality Monitoring System, Mark I Series. The instrument has a company specificity of $\pm$ 0.2 mmho cm^{-1} and $\pm$ 0.1 C, respectively. Salinities were computed from the measured conductivity and temperature values, using unpublished tables prepared at the Chesapeake Bay Institute. The associated precision in the computed salinity values is no worse than $\pm$ 0.1 ppt. In a manner similar to the velocity analysis, the depth-averaged salinities, $\overline{S(t)}$, were determined from the vertical salinity profiles. These values varied both spatially and temporally, and a pattern is only apparent in the net or time-averaged distribution of depth-averaged salinities, $\langle S(t) \rangle$ (Fig. 3).

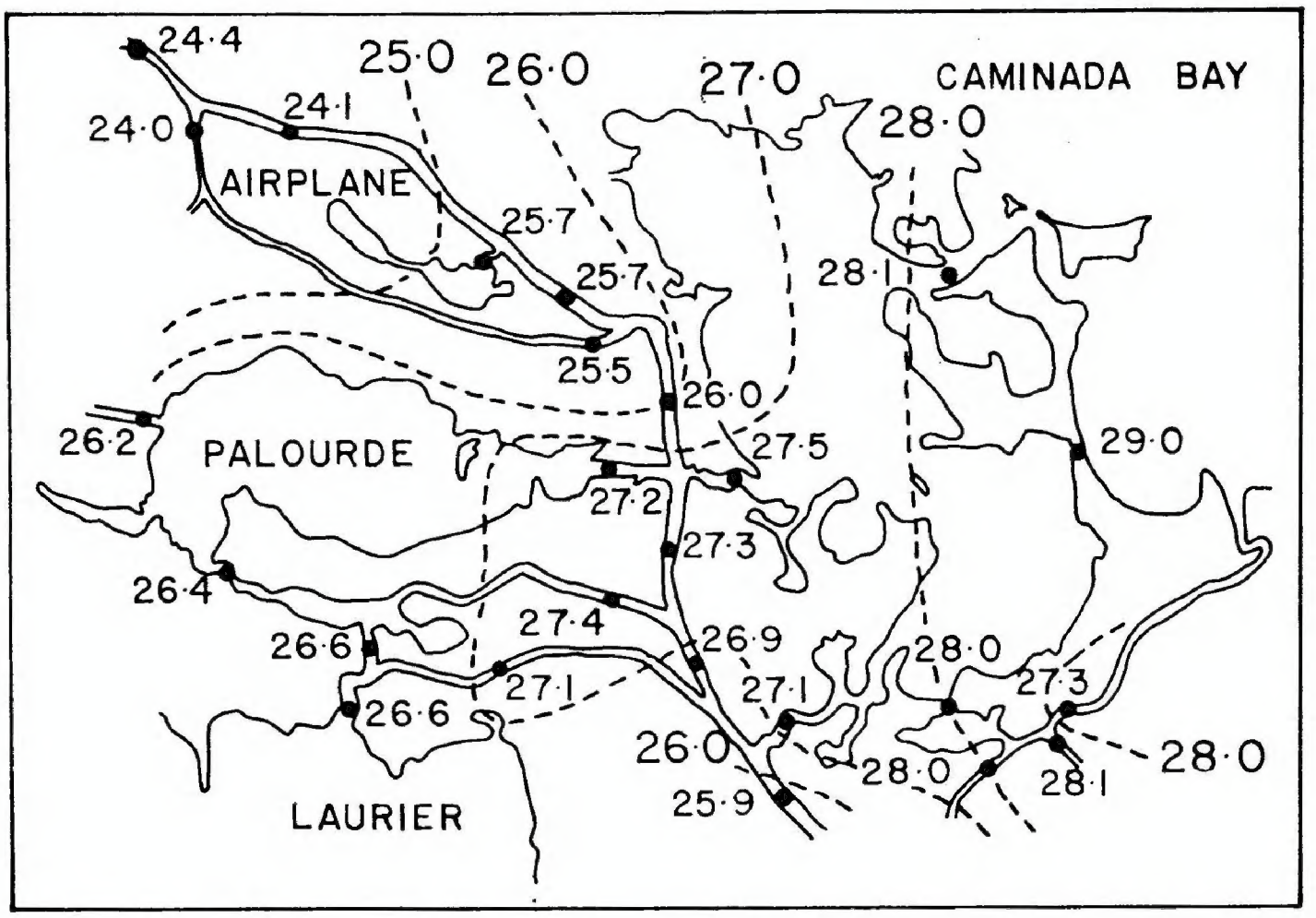

FIG. 3. Spatial distribution of net depth-averaged salinity (ppt).

The water level (Fig. 2) was recorded digitally at station 13 at the entrance to Airplane Lake every 15 min, using a Fischer and Porter Water Level Recorder 1542. The mean sea level during the study was approximately 30 cm below the typical summer mean sea level. The average tidal range for the study period measured 36 cm and the r.m.s. water level fluctuation from the mean was 5 cm.

The wind speed and direction were also recorded digitally every 15 min at station 13, 5 m above the mean water level, using a Climate CI-9C Wind System. Surface shear stress values were computed (Wu 1969) for each of the wind speed recordings. The resultant wind velocity was 1.06 m s^{-1} from 244°T, and the resultant wind stress was 0.07 dyne cm^{-2} from 245°T. The mean wind was 1.71 m s^{-1}, and the mean stress 0.12 dyne cm^{-2}. The r.m.s. deviation from the mean wind speed was 2.32 m s^{-1}, and the r.m.s. deviation from the mean stress measured 0.29 dyne cm^{-2}.

NET DISCHARGE COMPUTATIONS

Time averaged (net) discharge is a most useful parameter in indicating the overall circulation pattern in this complex network of channels. In general, the net discharge is difficult to determine as the velocity varies irregularly in a channel cross-section and changes with time. To estimate the net discharge, the following procedure was developed and applied to the collected data.

First, assume that the cross-sectional velocity distribution, at all times and depths, is parabolic with zero velocity along the levees. The parabolic shape of the lateral velocity distribution has been verified at stations 2, 18 (Kjerfve 1972) and 13 (Hacker 1971) during different tidal stages at several depths.

At any one time, let the velocity through the cross-section, the y-z plane, be $U(y,z)$ and let $V(z)$ be the measured velocity in mid-channel as a function of depth. The parabolic assumption yields

$$y^2 = -4p\,\{U(y,z) - V(z)\} \tag{1}$$

where p is the "distance" between the parabola vertex and focus with dimensions {LT}. As the velocity vanishes along the side boundaries, $y = \pm\, b(z)$, it follows that

$$U\,\{\pm b(z),z\} = 0 \tag{2}$$

which combined with (1) yields

$$U(y,z) = -\frac{V(z)}{b(z)^2}\,y^2 + V(z) \tag{3}$$

Integration of equation 3 with respect to y from $-b(z)$ to $b(z)$ followed by integration with respect to z from surface, $z = 0$, to the maximum depth, $z = d$, results in an expression for the cross-sectional discharge Q,

$$Q = \frac{4}{3}\int_0^d b(z)\;V(z)\;dz \tag{4}$$

Next, assume that each cross-section has a triangular shape with the deepest point in the middle of the channel. Kjerfve (1972) determined the bathymetry across the bayous at each station and showed that most cross-sections exhibited an almost triangular shape making this an acceptable assumption. If the bayou width at the surface is given by 2B, it follows that

$$b(z) = B - \frac{Bz}{d} \tag{5}$$

Substitution of $b(z)$ into equation 4 yields

$$Q = \frac{4B}{3}\left\{\int_0^d V(z)\;dz - \frac{1}{d}\int_0^d z\;V(z)\;dz\right\} \tag{6}$$

from which the discharge at any time can easily be computed numerically from the vertical velocity profiles or graphically using a planimeter. It should be noted that the first integral in equation 6 times the factor $\frac{4B}{3}$ would be the discharge in a rectangular cross-section, whereas the second integral is a correction factor due to the triangular channel shape.

The net discharge $<Q(t)>$ at each station was obtained by using a planimeter on plots of discharge *vs.* a mean tide period of 24.3 hours. Positive discharge values indicate ebb directed flows and negative values flood currents. The resulting net discharge at the 25 stations is shown in Fig. 4, and the discharge values for each station and stage are presented in Table 1.

TABLE 1

Mean discharge values ($m^3\ s^{-1}$) for each stage and station and net discharge and flow direction for each station. Values denoted * have been interpolated. Plus values indicate ebb flows and negative values flood currents. The net discharges are not arithmetic averages of the six stage values but were obtained graphically from plots of discharge *vs.* time.

Station Number	Stage 1	Stage 2	Stage 3	Stage 4	Stage 5	Stage 6	Net Discharge	Ebb Flow towards
1	8.5	8.7*	3.0	- 3.0	-12.1	- 9.9	-0.4	SE
2	1.1	0.5	0.0*	- 0.4	- 1.4	0.5	0.1	NW
3	7.4	7.5*	5.5	0.0	- 7.0	- 5.9	1.2	NE
4	34.7	69.6	19.4	3.5	-51.9	-59.8	4.9	E
5	40.6	62.8	30.0	26.2*	-90.8	-90.8	1.8	E
6	14.7	66.7	48.8	20.3	-35.8	-57.7	7.2	E
7	8.2	4.0	0.7	0.0	- 3.7	- 4.0	0.8	S
8	1.1	1.0	0.0	0.0	- 0.6	- 0.7	0.1	E
9	5.2	3.8*	1.0	0.0	- 2.8	- 3.3	1.0	SE
10	0.7	1.3	0.0	0.0	- 0.5	0.5*	0.5	SE
11	- 0.1	0.2	0.0	0.0	0.2	0.1*	0.1	S
12	0.8	0.5*	0.0	0.0	1.2	1.2*	0.5	SE
13	2.3	1.0	0.0	0.0	- 1.5	- 0.3	0.3	NE
14	23.4	31.3	17.3	16.4	-31.3	-37.1	3.8	E
15	2.4	2.7	2.4	1.9	- 1.9	- 3.5	0.6	E
16	10.3	10.3	9.7	6.4	-15.7	-14.0	2.1	NW
17	12.3	10.2	11.4	6.6	-15.0	-14.0*	3.1	N
18	24.9	38.4	16.0	12.8	-35.6	-44.0	3.0	N
19	5.7	6.0	4.5	2.4	- 8.7	-10.5	0.1	NE
20	1.1	2.7	1.1	1.1	- 2.7	- 3.5	0.0	NW
21	12.0	12.0	7.9	4.7	-14.3	-16.0	1.8	SE
22	4.1	15.4	8.1	6.6	-11.8	-17.3	1.1	N
23	0.0*	1.5	0.0	0.0	- 1.5	0.0	0.0	SE
24	4.1*	12.8	10.2	0.0*	-11.5	-10.2	0.8	NE
25	0.0	- 0.3*	- 0.7	- 1.0	- 1.4*	- 0.2	-0.5	S

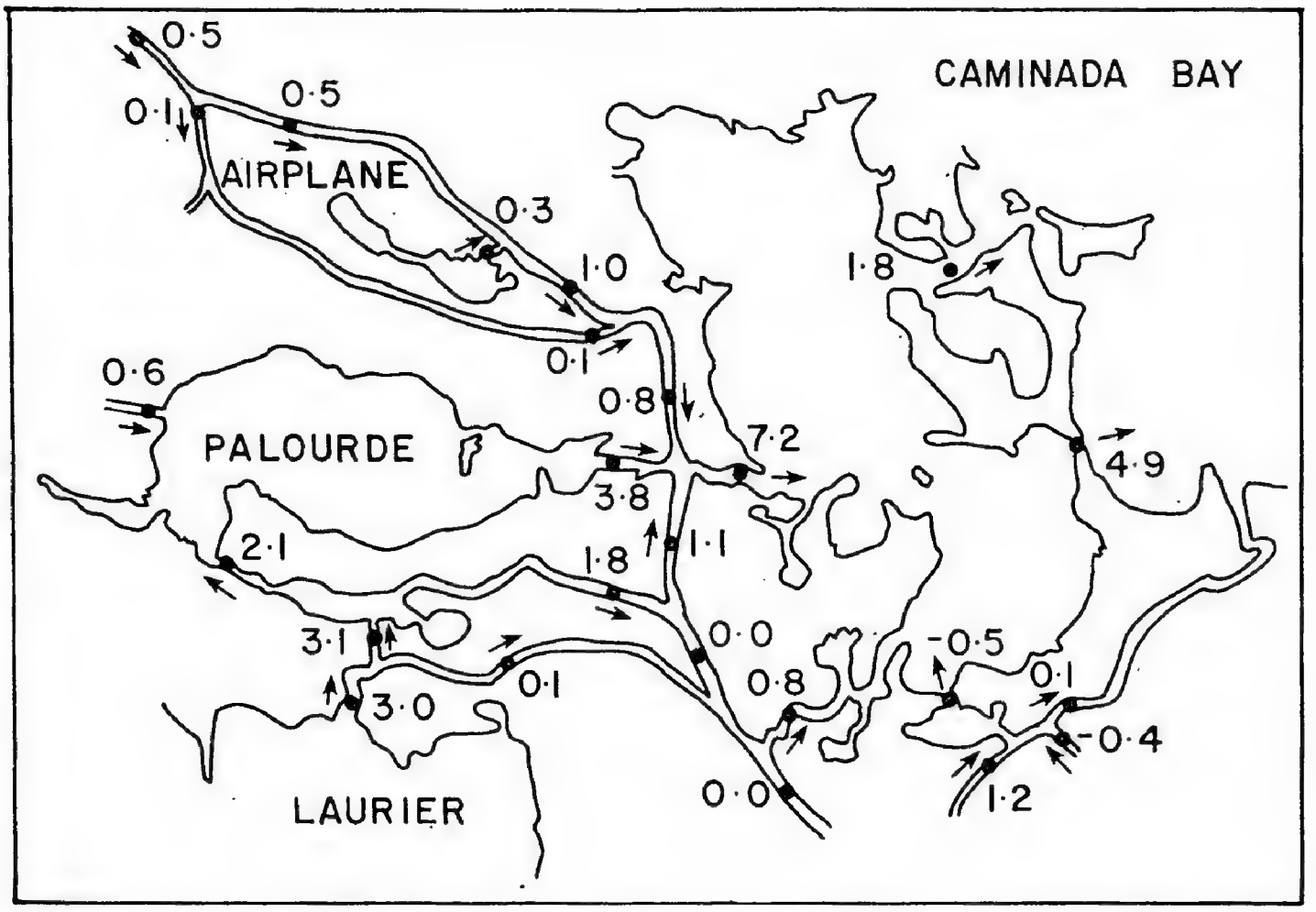

FIG. 4. Net discharge ($m^3 s^{-1}$) and flow direction in the study area.

As can be seen in Table 1, net discharges are small compared to peak instantaneous values. Computed coefficients of variation (Snedecor and Cochran 1967, pp. 62–65) are typically 1500%, which raises the usual question of the reliability of the calculated net discharges. Although net discharges do not balance exactly at bayou junctions (Fig. 4), differences between inflows and outflows are moderately small. E.g. at the junction controlled by stations 6, 7, 14, and 22, the difference between inflow and outflow is 23% of the total mean discharge at that junction. Similarly, the error is 32% at stations 7, 8, and 9; 6% at stations 17, 18, and 19; and in the case of Bay Macoin, the inflow is completely balanced by the outflow. The small errors are encouraging and point to the usefulness of the developed technique in computing net discharge values under the existing conditions.

DISCUSSION

The Airplane Lake study area, with a maze of bayous, estuarine lakes, embayments, lowlying *Spartina* marshes, and occasional mangrove (*Avicennia*) stands, does not represent a unique environment. Rather, this area is typical of a large portion of the wetlands of coastal Louisiana. Oil exploration and oil support operations along the Cajun coast have resulted in construction of criss-crossing pipelines, barge canals, dikes, and spoil banks. However, few if any environmental considerations have in the past been taken into account in the alteration

of the wetlands. It seems that the overall flow pattern and salinity distribution of an area should be given consideration, prior to any dredging or canal construction as these factors largely control the functioning of the ecosystem.

The water bodies in the study area are extremely shallow, with an area-weighted mean depth of approximately 0.5 m, making boating difficult in most of the bayous and lakes. The average channel width at the stations was 55 m and ranged from 15 to 145 m. Stations were located in the major bayous thought to have the greatest flow. The average water depth at mid-tide for the 25 stations was 1.9 m with the 7.1 m channel through Leon's cut at station 4, representing the maximum depth. Incidently, around 1960, Leon's Cut did not exist. It formed as a result of local fishermen lifting and pulling their flat bottomed boats across the narrow marsh-tongue. When the marsh was finally breached, the channel quickly widened and deepened. As a result, the circulation of the region probably changed drastically, particularly in view of the large flow through the cross-section at station 4 (Fig. 4 and Table 1).

The freshwater discharge into the bayou system, is quite low as indicated by the low net discharge values (Fig. 4). Also, the relatively high salinity values coupled with a gradual salinity gradient (Fig. 3) support this observation. It appears that most of the run-off enters the system from the northwest through Bayou Ferblanc, with some freshwater flow coming through William Canal (station 15).

In spite of the modest tidal range, 36 cm, the intertidal volume measures slightly more than 25% of the total water volume at mean tide. This is a rather high value, which e.g., may be compared to 11.3% for Chincoteague Bay (Pritchard 1960). The large prism for the Airplane Lake system points to the importance of the diurnal tide in mixing. In fact, it is possible to compute a value for the effective horizontal diffusion coefficient, K_H, using the one-dimensional diffusion equation averaged over one or more diurnal tide cycles,

$$S_f = \langle Q(t) \rangle \langle \overline{S(t)} \rangle - AK_H \frac{\delta \langle \overline{S(t)} \rangle}{\delta x} \qquad (7)$$

(Stommel 1953, Bowden 1963) where S_f is the net salt flux through the cross-sectional area A, equal to the difference between advective and diffusive fluxes, and the coordinate x is aligned along the bayou. On the assumption that the area is experiencing steady state conditions, S_f vanishes. It is then possible to solve for K_H, which was found to be 7×10^2 m^2 s^{-1} in Bayou Ferblanc (stations 7, 9, 10, and 12) and 14×10^2 m^2 s^{-1} in Lake Palourde (stations 14, 15, and 16).

It is somewhat surprising that these K_H values are one order of magnitude greater than those calculated by Bowden (1963) for the Mersey estuary where the tidal range exceeds 6 m, the tidal prism percentage is approximately 25%, and there exists a well developed gravitational circulation. With respect to Bayou Ferblanc, the K_H value is probably inflated, since salty Caminada Bay water can enter the bayou northwest of station 12 and advect downstream with the net current. This partially explains the large difference in effective horizontal mixing

between Bayou Ferblanc and the Mersey estuary. However, it does not explain the excessive mixing in Lake Palourde. Palourde with a large open surface area and extremely shallow depths has a depth to width ratio of 10^{-4} whereas both Bayou Ferblanc and the Mersey estuary have similar ratios on the order of 10^{-2}. This, in addition to the absence of net vertical velocity and salinity gradients, implies the importance of wind-induced mixing in addition to tidal mixing in the large lakes.

The effectiveness of tide and wind in mixing the shallow Louisiana water bodies is further indicated by the almost non-existent vertical salinity stratification. The stratification parameter (Hansen and Rattray 1967), defined as the bottom to surface net salinity difference divided by the depth-averaged net salinity, did not exceed 0.04 and was usually below 0.01. The circulation parameter, defined as the ratio of net surface velocity to net depth-averaged velocity, was in all instances less than 1.5. This would classify the study area as a type 1a estuary, which implies that the upstream salt transport is entirely due to diffusion in the absence of gravitational circulation.

The resultant westerly wind in June, although fairly weak, is not the most common among summer conditions for the Barataria Bay region, which then usually experiences southerly winds driven by the Bermuda High pressure system (Leipper 1954). In fact, the low mean water level during the study period can be explained by a resultant westerly wind stress for more than a week preceding the study. The 6.4 $m^3\ s^{-1}$ net discharge from the study area (as defined by stations 1, 2, 4, and 5) is therefore probably greater than for normal June conditions.

ACKNOWLEDGMENTS

The field portion of this work was supported by the Louisiana State University Office of Sea Grant Development, which is part of the National Sea Grant Program, sponsored by NOAA, U. S. Department of Commerce. The University of South Carolina IBM 370/168 computer was used for all computations. I am indebted to Dr. W. G. Smith, Ms. A. Siripong, and E. M. Bishop, C. D. Walters, and A. A. Pusch for their able field assistance.

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PERIODIC PHENOMENA AT THE MOUTH OF THE MISSISSIPPI RIVER

WM. J. WISEMAN, JR., L. D. WRIGHT,[1] L. J. ROUSE, and J. M. COLEMAN

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ABSTRACT

Time series of temperature fluctuations, as well as aerial and satellite imagery, indicate the presence of periodic phenomena within the effluent from South Pass, Mississippi River Delta. Time scales on the order of 1 min and 15 min recur in both remotely sensed and *in situ* data, a fact which suggests that the same phenomenon is being measured. Vertical coherence estimates indicate this to be internal wave motion. Estimates of gross Richardson numbers are near critical; instabilities in the wave field are a possible mechanism for entrainment, but cannot account for all the required entrainment.

INTRODUCTION

The processes through which river water spreads and diffuses into ambient marine water determine the rate and pattern of effluent deceleration and, consequently, the pattern of sediment dissemination and accumulation and the dispersal of riverborne pollutants. The mouths of many of the world's rivers, notably the Mississippi, Danube, and Po, are characterized by pronounced pycnoclines. Previous investigations have indicated that entrainment of saltwater across the pycnocline plays the dominant role in effecting deceleration and dilution of the buoyant river effluents at times of salt-wedge intrusion into the river channels (Wright and Coleman 1971, 1974).

Theory and laboratory experiments suggest that saltwater entrainment is largely a consequence of the breaking of shear-generated waves at the pycnocline (Keulegan 1949, Ellison and Turner 1959); however, direct field documentation of these waves has heretofore been lacking. In addition to these interfacial waves, low-frequency periodic pulses are highly apparent on infrared imagery of river plumes (Wright *et al.* 1973). Studies of effluent dynamics and sedimentation conducted at the mouth of South Pass, Mississippi River delta (Fig. 1A), have led to the identification of periodic phenomena which exhibit a variety of frequencies and wave number vectors both in the South Pass effluent and in adjacent ambient water masses. These phenomena and their associated manifestations and possible causes are the subjects of this report.

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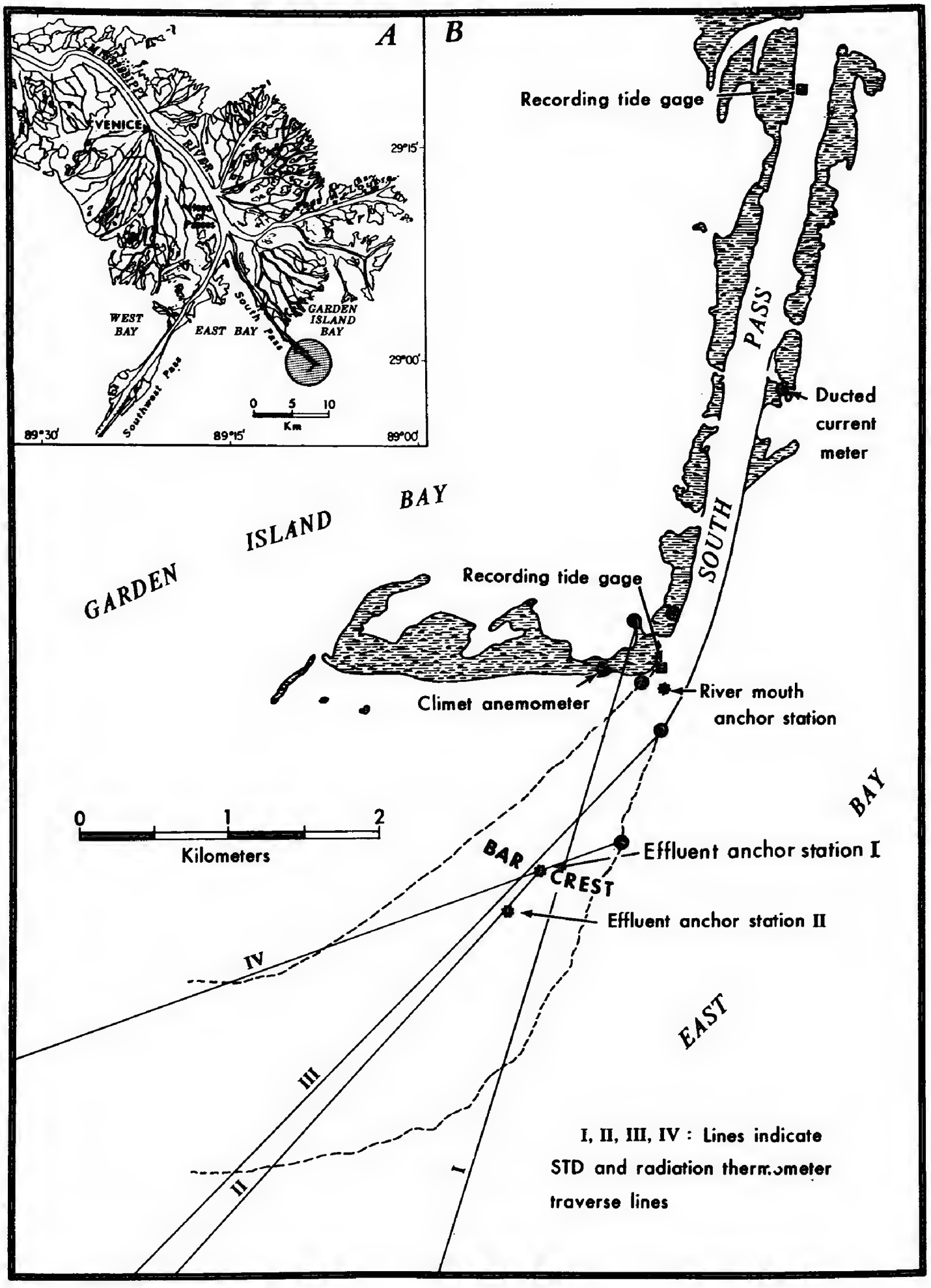

FIG. 1. A) (Inset) Location map; B) sensor deployment during field study.

FIELD TECHNIQUES

Remotely sensed imagery of the mouths of the Mississippi River (Fig. 1A) was obtained through the cooperation of NASA on five separate occasions (Earth Resources Aircraft Project missions 154, 159, 165, 191, and 194) from October 1970 through March 1972. The imagery included Reconofax IV and RS-14 thermal infrared (8–14-micron spectral band), color infrared (0.52–0.90-micron spectral band), and conventional black-and-white and color aerial photographs. This imagery was supplemented by photography with hand-held cameras made from light aircraft on numerous occasions from 1970 through 1973. During a 1973 field study (November 12–20), remotely sensed imagery (vertical and oblique photographs) was obtained from a Louisiana Department of Highways aircraft and from the LANDSAT satellite. Continuous surface temperature profiles in the South Pass effluent were made with a radiation thermometer (Barnes model PRT-5) mounted on the bow of a boat. Sensor deployment in and seaward of South Pass during the study is illustrated in Fig. 1B. Capacitance tide gages were installed at the mouth and at a position 4 km upstream. Salinity and temperature profiles were made within the channel during both flooding and ebbing tidal phases and within the effluent along the profile lines shown in Fig. 1B. Anchor stations in the mouth, over the bar crest, and seaward of the bar crest (Fig. 1B) were occupied continuously for periods ranging from 3 to 21 hours, during which time thermistor-chain, STD, and current-meter records were obtained.

Water salinity and temperature were measured in situ with Beckman induction salinometers and an InterOcean CSTD. Currents were measured by means of Bendix Model Q-15 ducted current meters and Hydro Products Savonius-type current meters. Offshore sampling positions were determined by horizontal sextant angles and shipboard radar. Temporal variations of the internal thermal structure were monitored with a chain of six thermistors linked to a six-channel Brush recorder. The thermistors used were manufactured by Yellow Springs Instruments Co. (Type 44030). The system was designed for a total range of —2 C to 40 C, individual spans of 1.5, 3, or 6 C at any one setting, and an accuracy, allowing for nonlinearity, of ± 0.02 C. The thermal time constants of individual sensors varied from 10 to 20 seconds.

THE LARGE-SCALE FLOW REGIME

The Mississippi River discharges sediment-laden freshwater into the Gulf of Mexico at rates which range, in an average year, from about 8,400 $m^3\ sec^{-1}$ at low stage to more than 28,000 $m^3\ sec^{-1}$ at flood stage. This river water is debouched into the Gulf in the form of numerous effluents which issue from the mouths of the delta distributaries and crevasses in the fashion illustrated in Fig. 2. Approximately 15% of the total Mississippi River discharge exists through South Pass. South Pass is 21.7 km long; it averages 240 m wide and 11 m deep. The cross-sectional area at the mouth is 2,324 m^2. Under normal conditions the effluents and ambient water masses tend to remain discrete, separated by pronounced density fronts.

The tides in the vicinity of the Mississippi Delta are diurnal and have a low range (less than 60 cm) and fortnightly variation. Inshore along the delta coast, tidal currents having velocities as high as 0.6 m sec^{-1} accompany tropic tides.

The combination of small tide range, appreciable river discharge, and deep distributary channels favors intrusion of seawater into South Pass as a pronounced salt wedge. The position of the toe of the wedge, though, migrates within the pass with the stage of the tide. Only during times of river flood is the salt wedge completely flushed from the channel to a position seaward of the distributary mouth bar (Wright 1970, 1971; Wright and Coleman 1971, 1974).

FIG. 2. ERTS—An image of Mississippi River delta, November 17, 1973 (band 5).

Because of the strong density contrasts and high Richardson numbers at the mouth and within the lower end of South Pass, during low and normal river stages buoyancy tends to be the dominant force controlling effluent expansion. At these times of salt-wedge intrusion, river outflow expands and thins progressively as a relatively homogeneous layer approximately in accordance with the buoyant expansion model described by Wright and Coleman (1971). Vertical entrainment of saltwater across the pycnocline, probably due to breaking internal waves, is presumed to be primarily responsible for seaward deceleration.

PERIODIC SURFACE PHENOMENA

Abrupt, periodic contrasts in turbidity, temperature, and surface roughness are apparent on the remotely sensed imagery of the waters near South Pass.

Examples of these features can be seen in the visible infrared (0.52–0.90-micron spectral band) (Fig. 3) and thermal infrared (8–14-micron spectral band) (Fig. 4). At least four major types of repetitive features can be consistently identified: regularly spaced, pulselike fronts aligned perpendicular to the direction of flow within the effluent (type I); irregular, short-crested, and more closely spaced wavelike features which occur within the effluent between the more conspicuous fronts (type II); linear, long-crested slicks oriented perpendicular to the general trend of the delta front (parallel to the effluent) within both the effluent and the ambient water (type III); and slicks similar to type III, except oriented parallel to the delta front (perpendicular to the effluent) (type IV). Features of types I and II are confined to the main effluent, whereas types III and IV are ubiquitous.

FIG. 3. Near-infrared photo of South Pass plume showing periodic surface features on May 16, 1971 (NASA EOAP Mission 165).

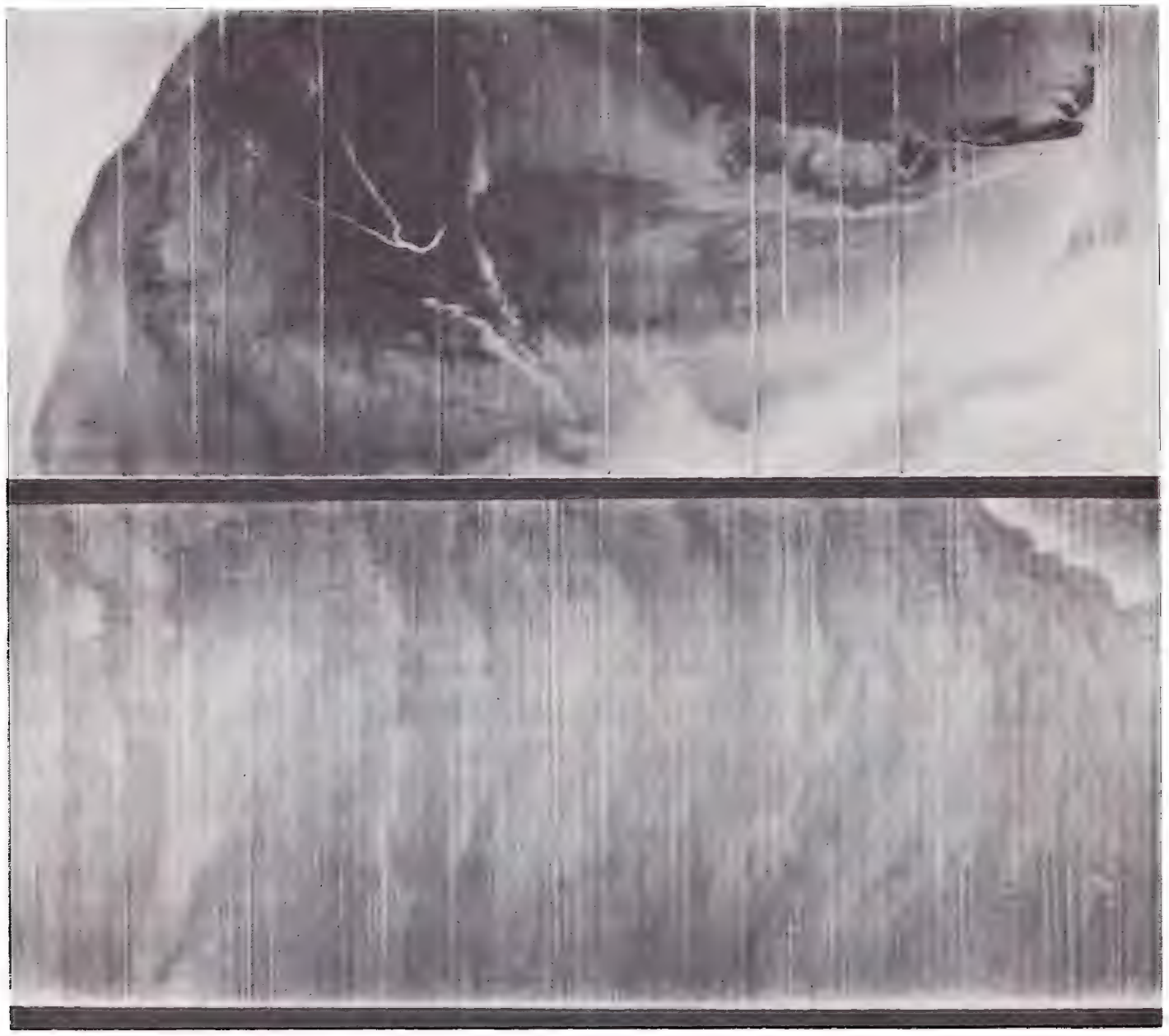

FIG. 4. A) Thermal infrared photo of South Pass plume showing periodic surface features on May 16, 1971 (NASA EOAP Mission 165); B) low-level image from same area.

At the mouth of South Pass, type I fronts are evidenced by sharp changes in turbidity (Fig. 3) and temperature (Fig. 4). Detailed examination of Fig. 3 shows that each feature is characterized by a gradual decrease in turbidity in a landward direction; this decrease is followed by a very abrupt turbidity increase immediately landward (upstream) of the fronts. Similarly, the thermal imagery (Fig. 4) indicates a gradual warming (lighter tone) of surface water, followed by abrupt cooling in an upstream direction. At the time the imagery was made (mid-May 1971), river water was characterized by low temperatures relative to those of seawater. River water is always a high turbidity source. Thus, the pulse-like surface features appear to reflect alternating gradual partial emergence or mixing and abrupt submergence of the underlying saltwater. These patterns are consistent with those described for thermal plumes by Scarpace and Green (1973).

The fronts appear to be present during all tidal phases and at all river stages; however, they are most conspicuous during low river stage, when the pycnocline

is shallowest, and during the early part of ebbing tide, when outflow is undergoing acceleration. Under high-river-stage conditions the features are evident only in the seawardmost regions of the effluent.

The fronts have long, regular, and gently arcuate crests which span the entire width of the effluent. The features shown in Figs. 3 and 4 are separated by intervals which range from 250 m to 450 m. A comparison between imagery made during flooding and ebbing tides on May 17, 1971 (mission 165), revealed that the separations averaged 390 m during flooding tide versus 280 m during ebbing tide. Consecutive imagery at intervals of 5 minutes and 9 minutes on this same mission indicated that the forms advanced seaward at velocities which averaged 0.4 m sec^{-1}. The observed length and velocity values suggest approximate periodicities ranging from 12 to 18 minutes. The mechanisms responsible for the generation of these pulses are presently unknown.

Between and parallel to these relatively low-frequency fronts, there are numerous less pronounced and more closely spaced forms which display short, discontinuous crests (type II features). Examples of these are shown in Fig. 4B, which is a low-level thermal image of a portion of the outermost region of the effluent from Fig. 4A. Normally these surface features appear only near the seaward extremes of the effluent (4–5 km from the mouth) where the depth of the pycnocline is 1 m or less. They appear to be highly ephemeral. Their irregular crest forms and transient nature make measurement of their wavelengths difficult; however, separations ranging from 10 to more than 100 m can commonly be discerned. It is our opinion that these more closely spaced temperature and turbidity variations are the surface expressions of the internal waves to which vertical entrainment has been attributed.

The details of surface temperature variations in the South Pass effluent are perhaps most effectively illustrated by a radiation thermometer profile from November 18, 1973 (Fig. 5). This profile shows both the high-frequency internal wave features and the lower frequency fronts. Three salient features are evident from the profile: sharp, rapid temperature fluctuations and thermal amplitudes ranging to 1.0 C over lengths averaging 45 m* and presumably corresponding to surface expressions of internal waves; lower frequency oscillations in mean temperature and in the amplitudes of the higher frequency features, likely reflecting the pulselike fronts; and an overall seaward increase in absolute mean surface temperature, testifying to the progressive dilution of the cool freshwater effluent by warmer seawater entrained from beneath the pycnocline.

The features referred to as types III (Fig. 3) and IV (Fig. 6) appear to be basically identical except with respect to their orientations. These long-crested wave forms have several aspects to their surface expressions. They are often highly apparent to the naked eye and to conventional photography owing to sharp turbidity contrasts (e.g., Fig. 3). Equally strong temperature changes are also characteristic: The intersection of the radiation thermometer profile (Fig. 5)

* Wavelengths were determined from the Doppler equation and PRT-5 transects made steaming with the current and against it.

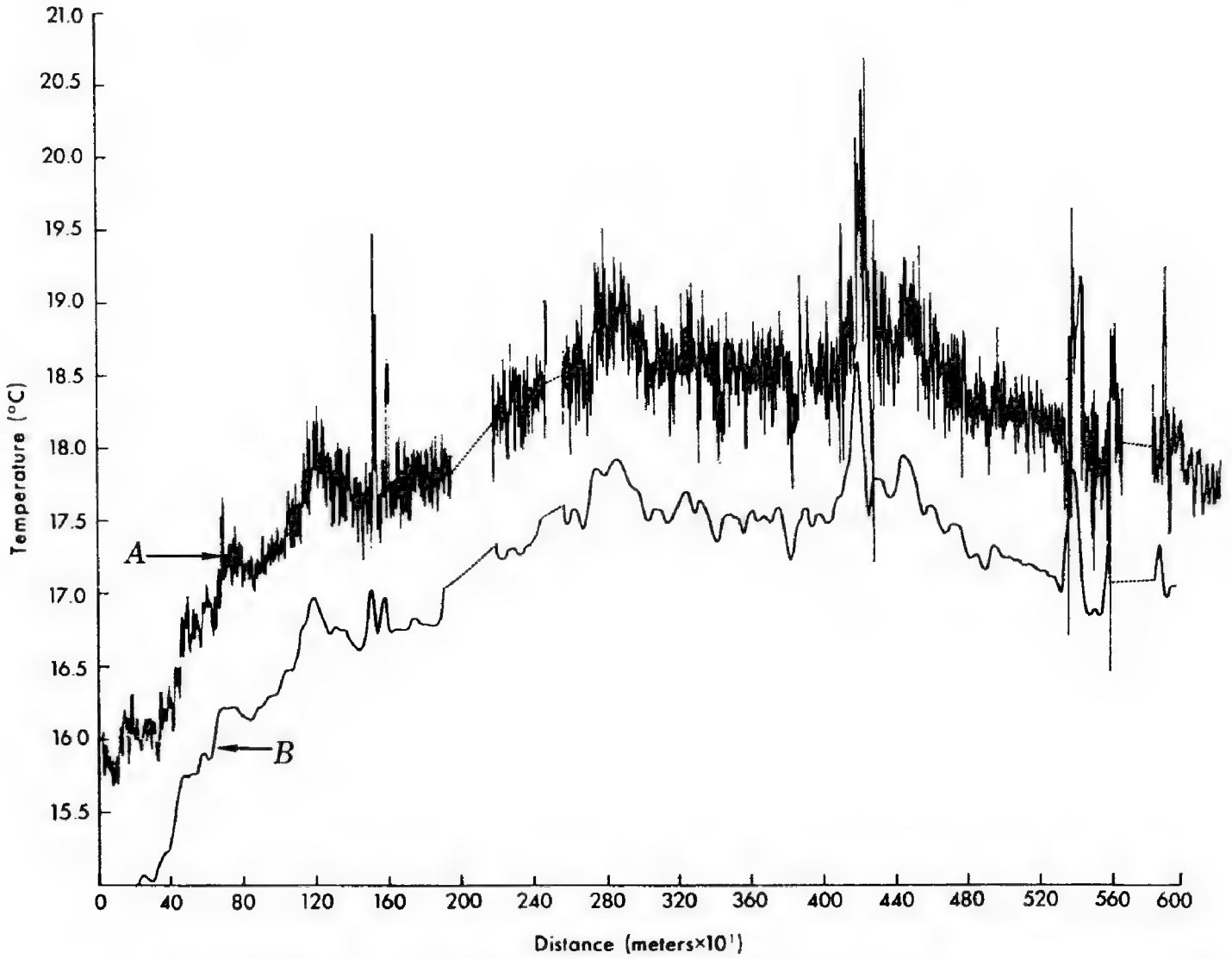

FIG. 5. A) Temperature section along South Pass effluent plume on November 18, 1973, using PRT-5 infrared sensor; B) low-pass-filtered version of 5A offset vertically by —1 C.

with a group of these forms near the seaward extremes of the South Pass effluent (at a distance of 5,400 m) is marked by temperature fluctuations as high as 3 C in amplitude. Unlike features of types I and II, however, types III and IV are frequently distinguished by appreciably reduced surface roughness, which causes them to appear as "slicks" similar to those which often characterize large-scale internal waves over the continental shelf (LaFond 1962; Vernon Pidgeon, personal communication 1974). In addition, light shadowing effects and differences in the angle of sun reflection such as those seen in Fig. 6 suggest that the forms may exhibit measurable surface relief; however, this has not been established by direct ground observations. Types III and IV tend to occur in broadly spaced groups 1 km or more apart but containing 3 to 10 individual waves. Upon encountering frontal water-mass boundaries, the waves and wave groups tend to accumulate or to be partially reflected; in many instances they fail to propagate beyond these boundaries.

The causes of these features remain to be determined. Type III features are parallel and appear to radiate from the effluent boundaries. Their general appearance in relation to the boundaries suggests that they may be Cauchy-Poisson

FIG. 6. Oblique aerial photo of type IV features at the mouth of South Pass on November 18, 1973.

waves (e.g., Kinsman 1965, pp. 199–219) or internal analogies thereof generated by alternating buildup and relaxation of head within the effluent.

Type IV wave forms are oriented roughly parallel to the delta front platform and are most abundant near the outer boundaries of the large-scale fresh and brackish water masses which surround the delta. Their relationships to these boundaries are very similar to the relationships between effluent boundaries and type III forms; low-frequency or aperiodic oscillations of head within delta-front freshwater masses may be responsible for their generation, although a seaward direction of migration appears to be most common. Occasionally these forms intersect the effluent. The effects are dramatic. In the case shown in Fig. 6, and in several other similar cases, intersection of the effluent boundary by type IV wave groups causes a series of offsets in the planar pattern of the boundary.

PERIODICITIES IN INTERNAL TEMPERATURE STRUCTURE

The various wavelike phenomena just described are not restricted to the surface. Thermistor chain observations of November 16–19, 1973, reveal subsurface oscillatory behavior. Records from within the South Pass channel, over the distributary mouth bar, and seaward of the bar shed considerable light on the nature of the periodic phenomena.

Continuous thermistor chain records were obtained in the South Pass channel, approximately 100 m upstream from the mouth, for a period of 2.3 hours (0803–1050 CST) on November 19. The tide was flooding at the time of the observations. Figure 7 shows vertical profiles of density (σ_t), temperature, and the Brunt-Väisälä frequency $N = [(-g/\rho)\ (\partial\rho/\partial z)]^{1/2}$, where ρ is density, g is the acceleration due to gravity, and z is the vertical coordinate. Figure 7 indicates that at the time of the observations the pycnocline was approximately at a depth of 2.5 m, where N had a value of 0.31 rad sec^{-1}. Temperatures ranged from 15.7 C in the upper layer to 22.5 C in the lower salt layer. In order to identify possible periodic oscillations in the thermal structure, thermistors were placed at depths of 1.9, 2.4, 2.9, 3.4, 3.8, and 4.3 m. The records from the thermistors do not accurately represent the thermal variations of the water but rather these variations filtered by the response of the thermistors. The impulse response of the

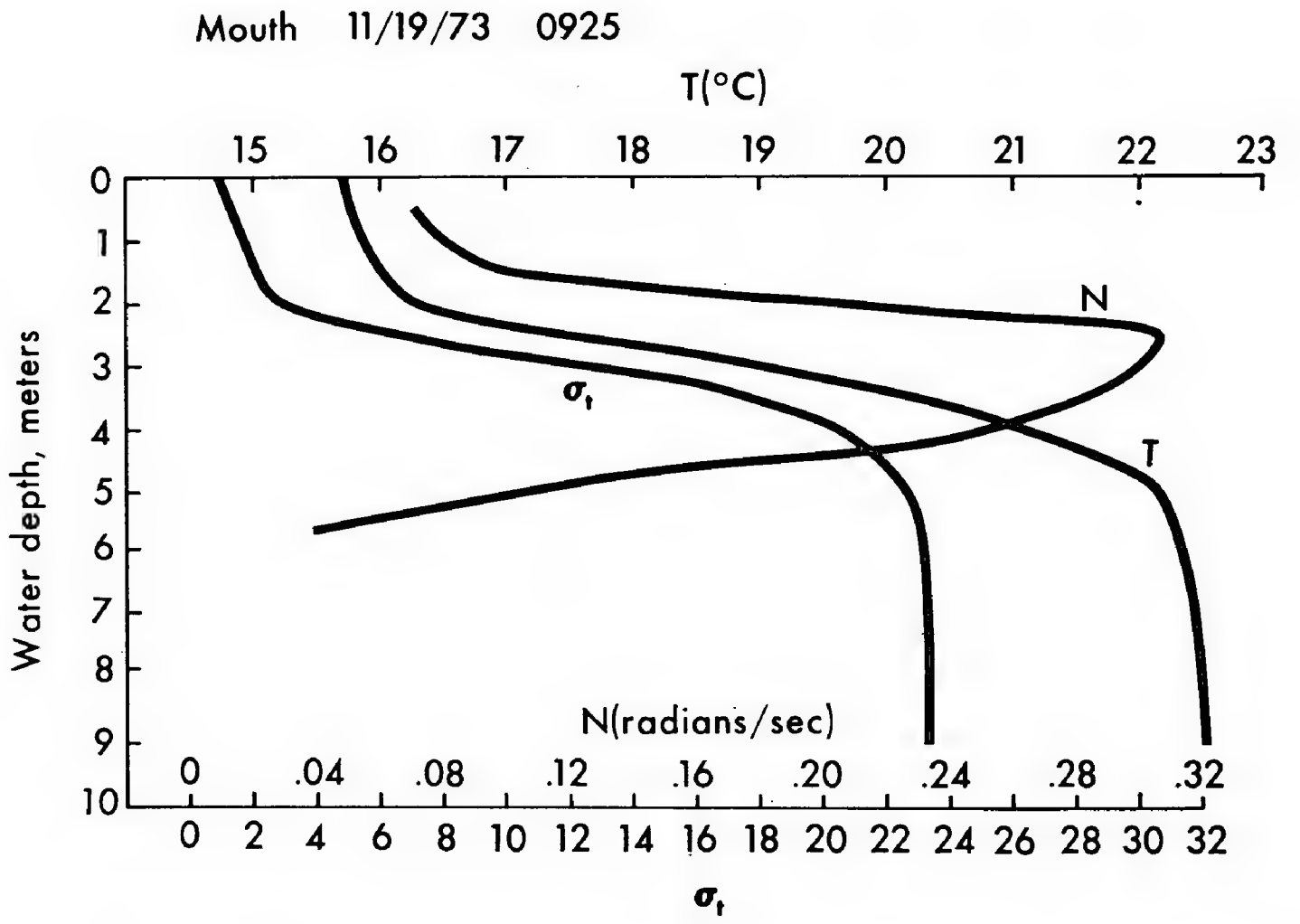

FIG. 7. Density, Brunt-Väisälä frequency and temperature profile inside South Pass on the morning of November 19, 1973.

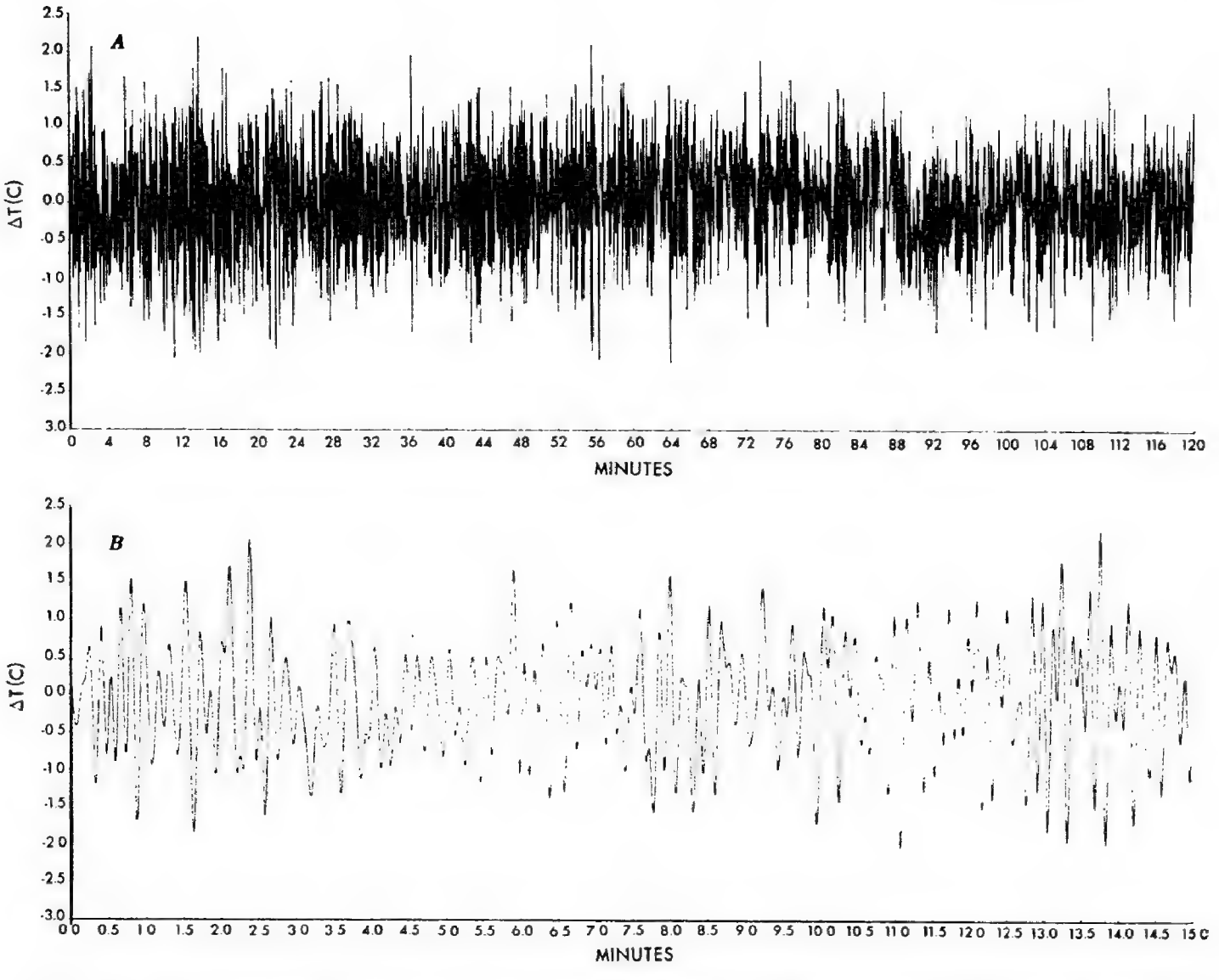

FIG. 8. A) Corrected, low-pass-filtered temperature record from near the pycnocline within South Pass; B) enlargement of a portion of 8A.

thermistors is exponential and the time constants are known, all being on the order of 15 sec. Therefore, the original thermal variations of the water can be recovered from the measured data by numerically applying the inverse filter of the one inherent in the thermistor response (Mason and Zimmermann 1960). Such a correction was applied to all the recorded data. A corrected, low-pass-filtered record from the 2.9 m thermistor is shown in Fig. 8A. Scale expansions of the first 15 min of the record are shown in Fig. 8B.

The highest thermal amplitude fluctuations appear in the 2.9 m thermistor record. Below this level temperature variations retain approximately the same general pattern but decrease progressively in amplitude.

The most conspicuous features of these records are the high-frequency temperature oscillations which occurred throughout the entire observation period. At times, the peak-to-peak amplitudes of these oscillations reached 3.6 C, indicating a vertical displacement of 1.3 m near the pycnocline.

Power spectrum analyses of selected records are shown in Fig. 9A. The records first had a mean and a linear trend removed, the first and last 10% of the records were cosine-belled, and discrete Fourier transforms of the records were computed using FFT. These were then averaged in blocks of 20, giving a frequency reso-

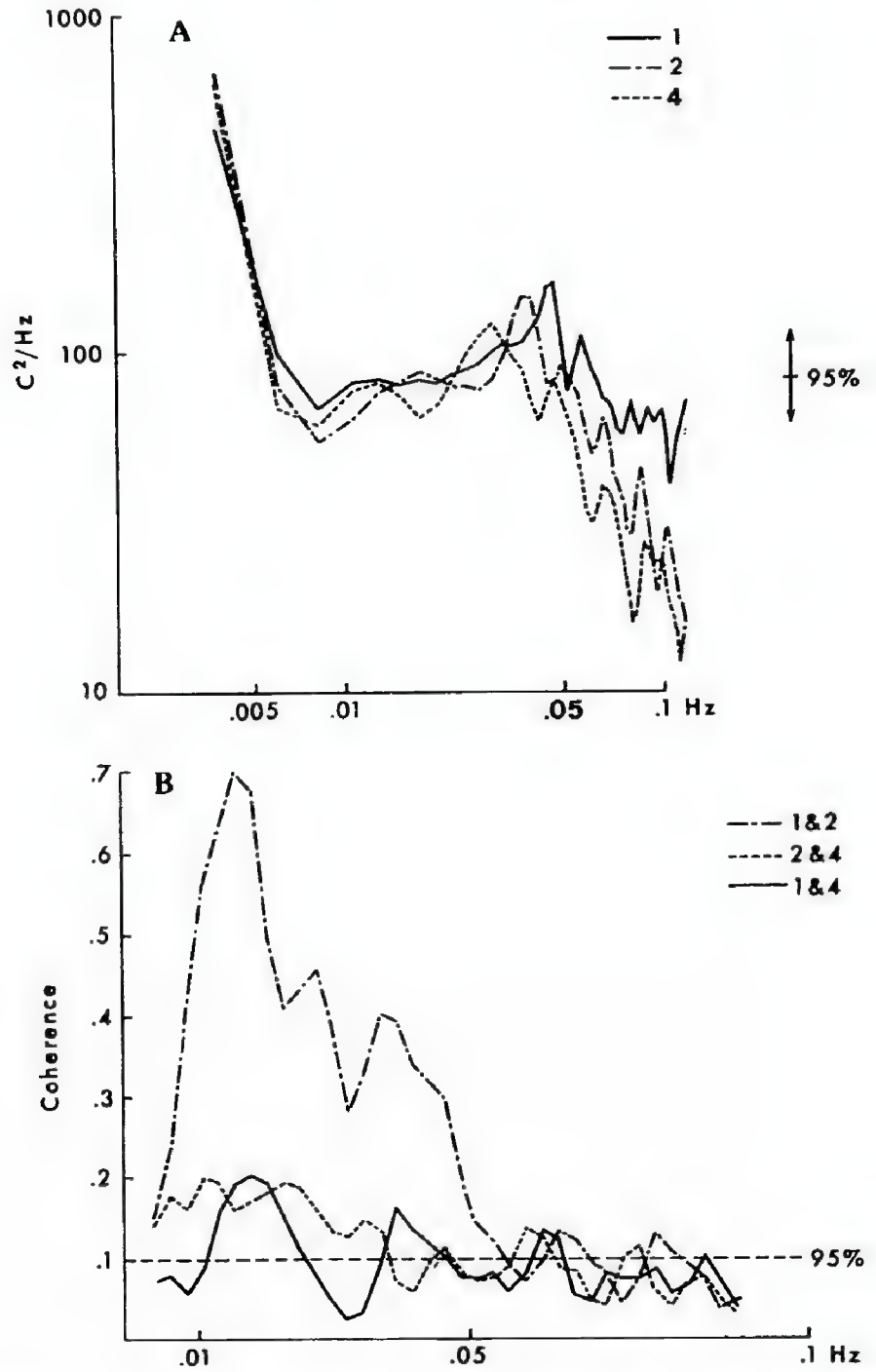

FIG. 9. Spectra (A) and coherence (B) estimates from records of temperature fluctuations made within South Pass. Ninety-five percent confidence and significance levels are indicated. Thermistors were at the following depths: 1:2.9 m, 2:3.4 m, 4:4.3 m.

lution of 0.0024 Hz, and "hanned" (Blackman and Tukey 1950) to improve stability. Coherence estimates were computed using the following formula:

$$r^2 = \frac{\{\Sigma(ac+bd)\}^2 + \{\Sigma(bc-ad)\}^2}{\Sigma(a^2+b^2) \cdot \Sigma(c^2+d^2)}$$

where (a, b) and (c, d) are the discrete Fourier coefficients of the two records, r^2 is the coherence estimate, and Σ represents an average over 20 spectrum components. The resulting estimates were also "hanned" to improve stability. Two Doppler shifts are present in our data: the frequency shift at one sensor relative to the signal at another sensor, which is due to the shear, and the shift in the observed frequencies relative to the true frequency of the temperature field. The

latter shift is due to the mean flow and cannot be corrected without a known dispersion relation. Our best estimate of the requisite corrections for all our data suggests that the frequencies of our peak spectrum estimates are high, but never by more than a factor of 2 and usually by much less.

In the three records shown, narrow and distinct spectrum peaks occur in a linear frequency band between 0.03 and 0.055 Hz. The peak tends to shift to lower frequencies at greater depth. This may possibly be a Doppler shift caused by the intense shear that was present during the measurements. The band of peak frequencies lies near the pycnocline Brunt-Väisälä frequency, a fact which suggests that these oscillations are indeed internal waves. Further justification of this interpretation is given by the coherence estimates, which rapidly drop to insignificant values at frequencies higher than this band (Fig. 9B). It should also be noted that there is a band of high coherence at frequencies near 0.017 Hz.

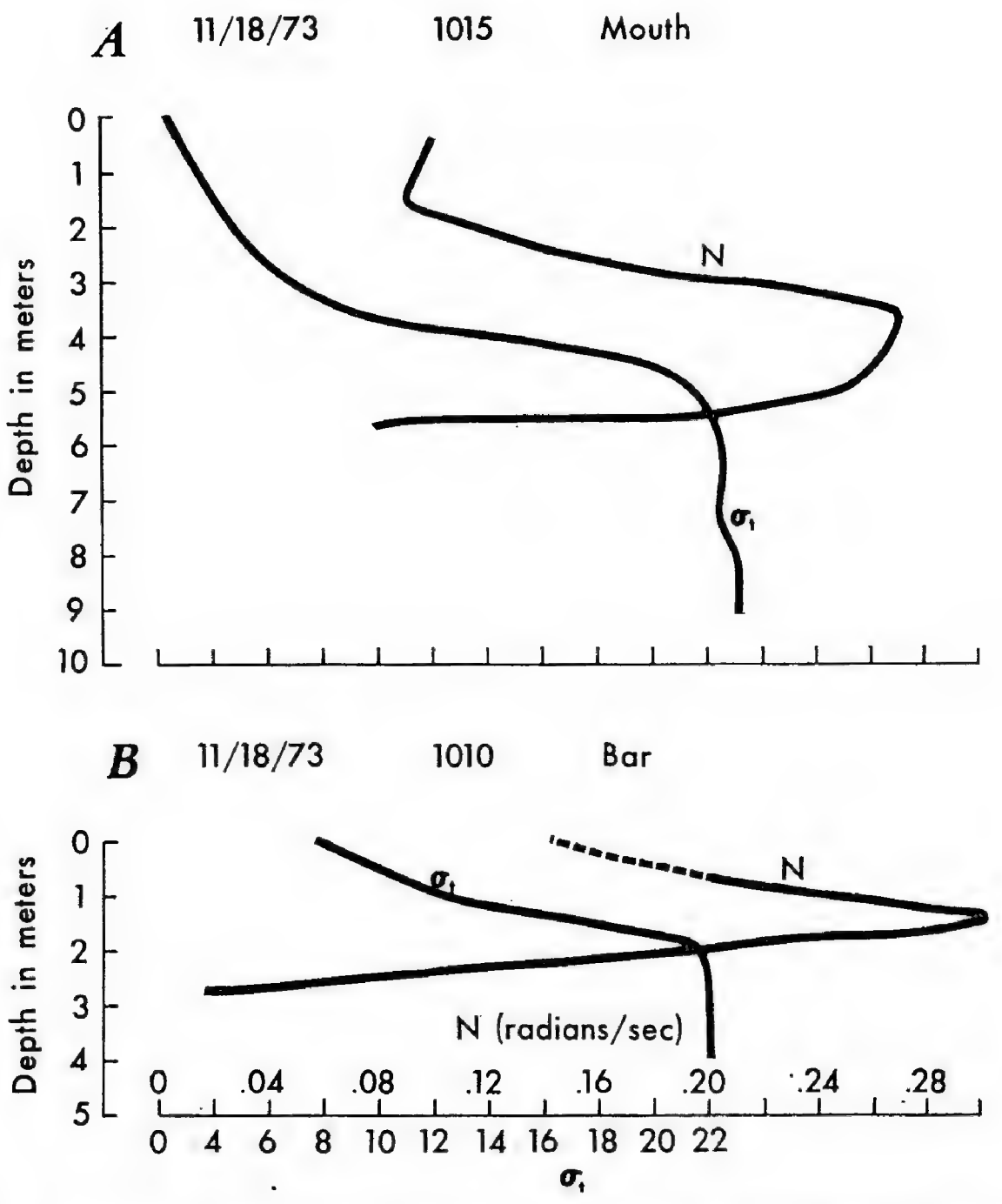

FIG. 10. Density and Brunt-Väisälä frequency profiles within South Pass (A) and over the bar (B) on November 18, 1973.

The relatively high frequency internal waves constitute the fundamental oscillations in the thermal time series. However, from Fig. 8A it is highly apparent that lower frequency variations in the thermal amplitude of individual internal waves, as well as in mean temperature, are present. The record shows bursts of high thermal variation at intervals of about 10 to 12 min. These bursts are accompanied by variations in mean temperature (i.e., the low-pass filtered temperature records), also at intervals of 10–12 min. This low-frequency alternate warming and cooling implies respectively upward and downward undulation of the pycnocline. It is our opinion that these low-frequency oscillations in pycnocline depth and internal wave amplitude correspond directly to the surface

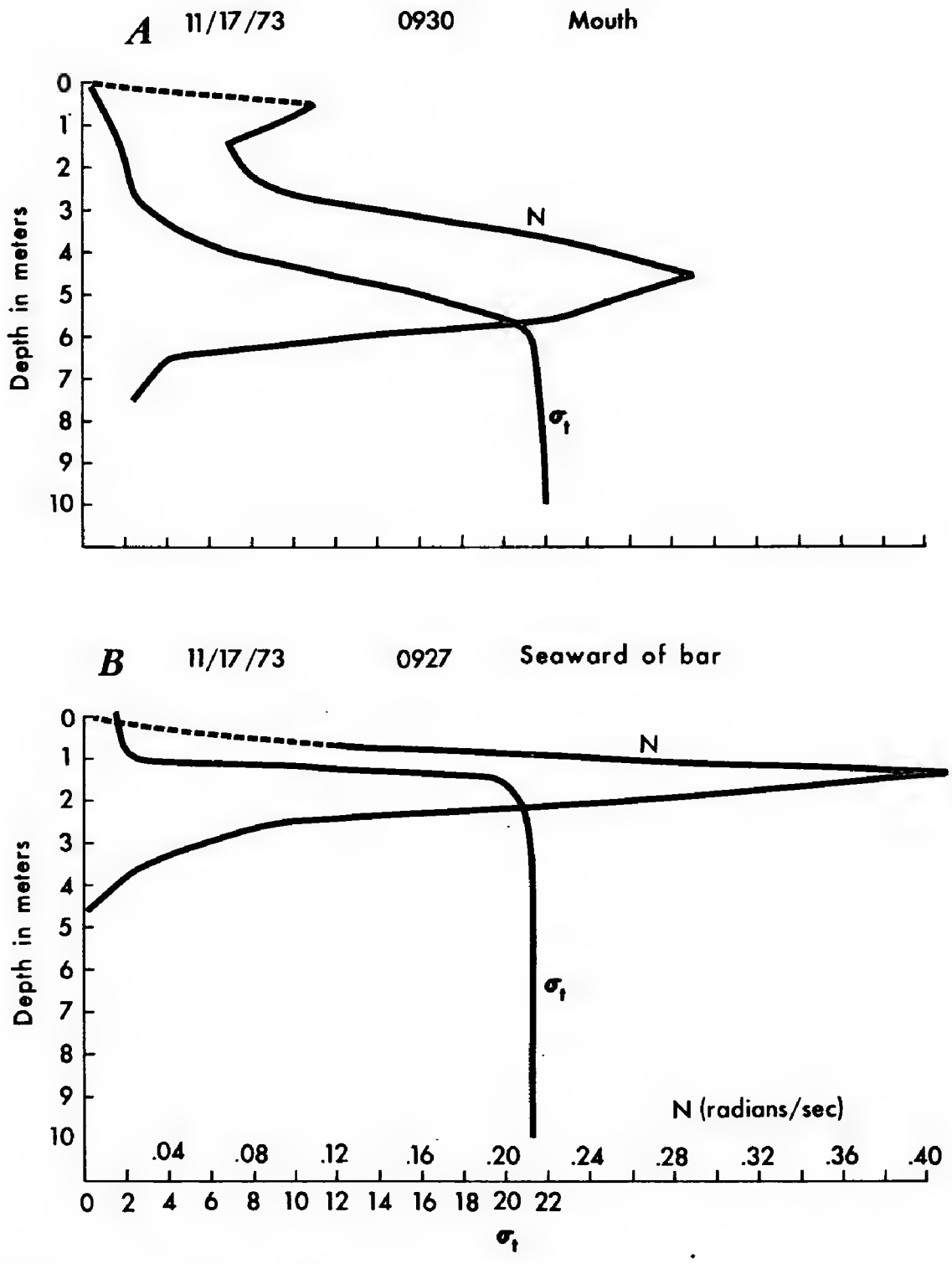

FIG. 11. Density and Brunt-Väisälä frequency profiles within South Pass (A) and outside the bar (B) on November 17, 1973.

pulselike phenomena exhibited by remotely sensed imagery. The implication is that the pulses originate within the distributary channel.

Sets of observations similar to those just described were also obtained over the crest of the South Pass bar on November 18 (effluent anchor station I) and seaward of the bar crest on November 16–17 (effluent anchor station II). Representative vertical profiles of σ_t, N for the two stations are shown in Figs. 10B and 11B. Profiles from the mouth at corresponding times are presented for comparison as Figs. 10A and 11A. Both stations show a pronounced decrease in pycnocline depth and an increase in maximum Brunt-Väisälä frequency over corresponding values at the outlet. As would be expected, the sharpest pycnocline and highest N occurred at effluent anchor station II, seaward of the bar crest, where vertical mixing is less pronounced. The gradient Richardson number, Ri, was approximated by

$$\mathrm{Ri}\ (\mathrm{d}) = \frac{-2g}{\rho(\mathrm{d}+1/2) + \rho(\mathrm{d}-1/2)} \frac{\rho(\mathrm{d}-1/2) - \rho(\mathrm{d}+1/2)}{1^{\mathrm{m}}} \Big/ \left(\frac{\mathrm{U}(\mathrm{d}-1/2) - \mathrm{U}(\mathrm{d}+1/2)}{1^{\mathrm{m}}}\right)^2$$

where g is gravity, ρ is density, U is speed, and d is a depth in meters. Over the bar Ri at the pycnocline had a near-critical value of 0.15. Seaward of the bar Ri had a value of 16, indicating stability.

Corrected, filtered thermistor records from a depth of 1.5 m at effluent anchor station I and from a depth of 2 m at station II are shown in Figs. 12 and 13,

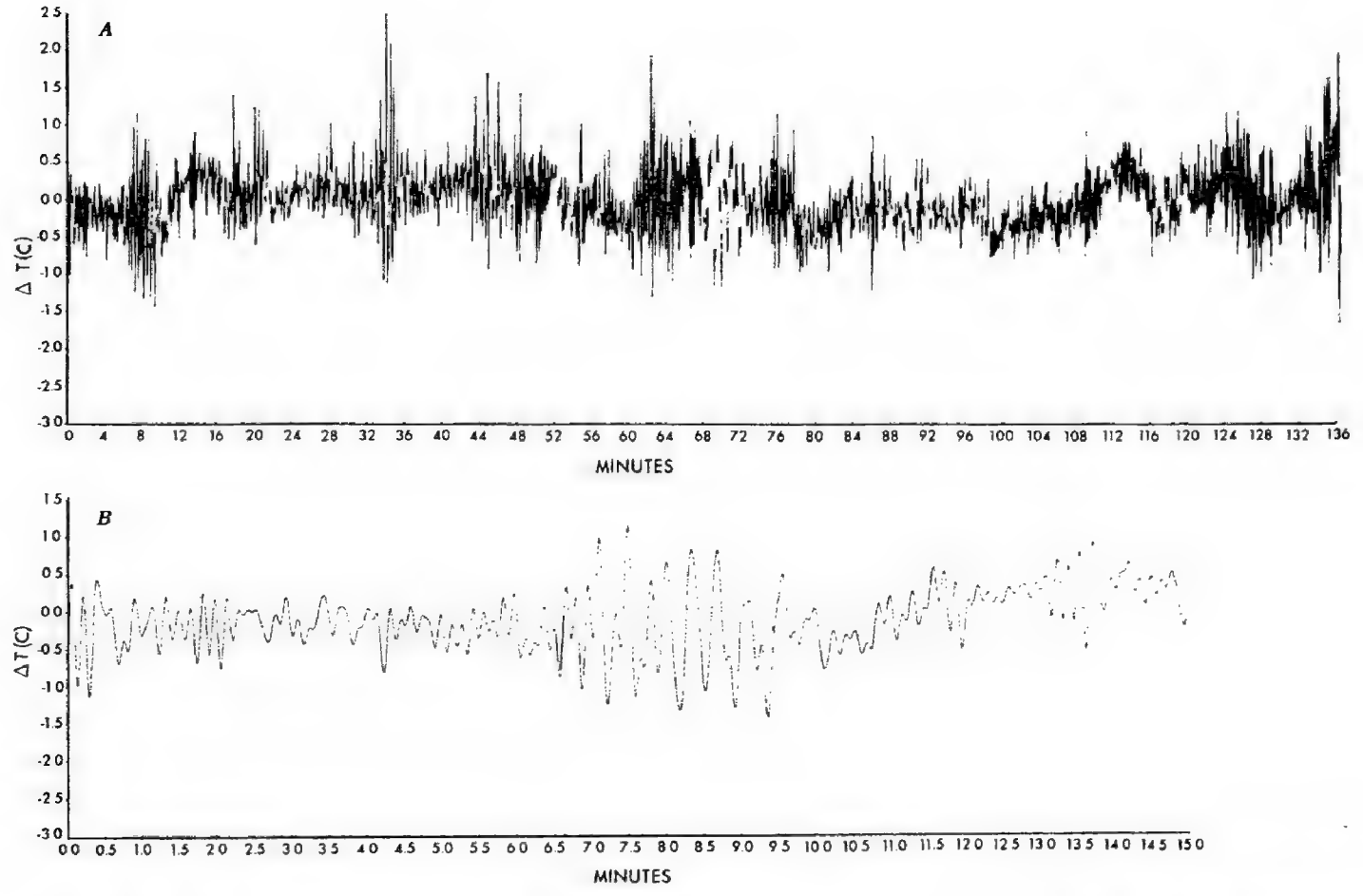

FIG. 12. A) Corrected, low-pass-filtered temperature record from 1.5 m depth over the South Pass bar; B) enlargement of a portion of 12A.

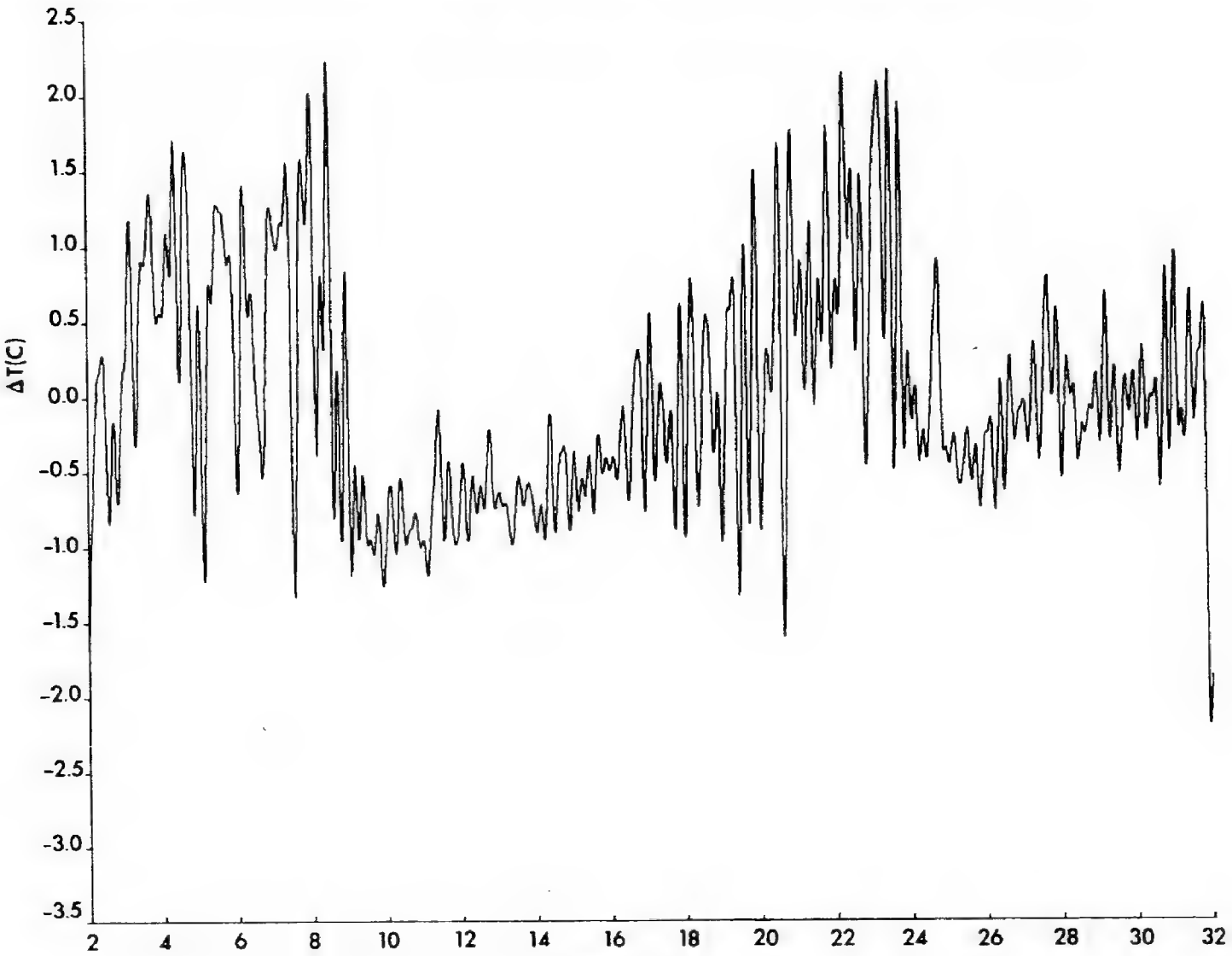

FIG. 13. A corrected, low-pass-filtered record of temperature from 2 m depth outside the South Pass bar.

respectively. At anchor station I, owing to the shallow water (3.5 m) over the bar crest, thermistors were situated at depths of 0.5, 1.0, 1.5, 2.0, and 3.0 m. Seaward of the bar, at station II, thermistors were more widely spaced.

Thermistor chain records from over the distributary mouth bar (Fig. 12) show pronounced temperature fluctuations, as in the case of the record from within the channel. The largest temperature oscillations were exhibited nearest the pycnocline, where ranges of more than 4 C were observed. Spectrum analyses of 2 hours of data from these records have a frequency resolution of 0.0028 Hz. A suggestion of a spectrum peak occurs at 0.07 Hz (Fig. 14A). The definition of the peak is severely hampered by the noise induced by the surface gravity waves that were present during the observations. This 0.07 Hz peak also appears on the coherence plots as a region of significant vertical coherence (95%) (Fig. 14B). At lower frequencies, both the power spectra (Fig. 14A) and the coherence estimates (Fig. 14B) suggest a vertically coherent, energetic motion at frequencies near 0.02 Hz. The local maximum Brunt-Väisälä frequency during the observations was estimated at 0.31 rad sec^{-1} (0.05 Hz). It is thus difficult to justify the motions at a frequency of 0.07 Hz as locally generated internal waves. A more

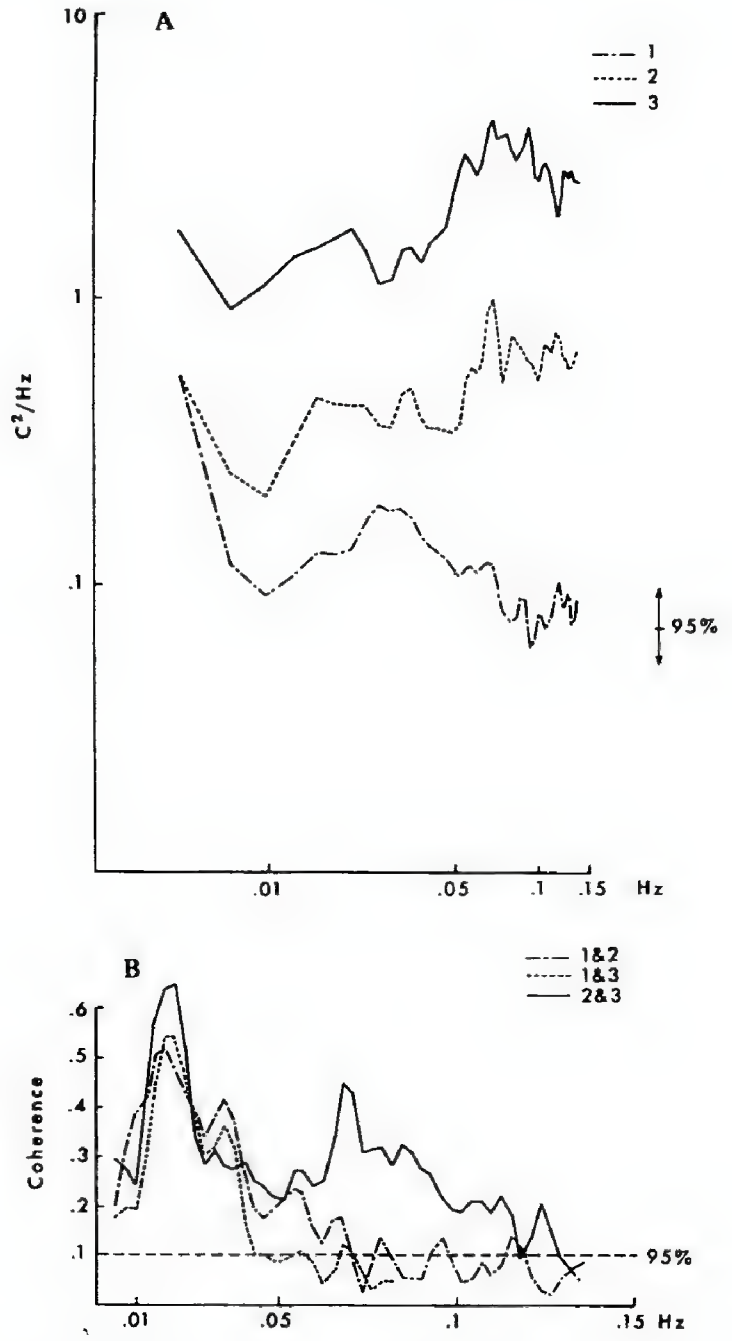

FIG. 14. Spectra (A) and coherence (B) estimates from records of temperature fluctuations made over the South Pass bar. Ninety-five percent confidence and significance levels are indicated. Thermistors were at the following depths: 1:0.5 m, 2:1.0 m, 3:1.5 m.

likely explanation is generation upstream of the recording station and advection into the region. No such difficulty exists with the motions at 0.02 Hz or with those associated with a third minor peak at approximately 0.033 Hz.

Two short but extremely interesting records were obtained from outside the river mouth bar on November 17 from 0914 to 0945 and from 0952 to 1023. The former was recorded at a depth of approximately 2 m and the latter at 2.5 m. Both records show bursts of temperature fluctuations occurring at intervals of 12 to 16 min (e.g., Fig. 13). Power spectra of these two records are shown in Fig. 15. The spectra were computed as described for the data taken inside the pass except that the spectrum estimates were averaged in groups of 5 rather than 20 before "hanning," giving a frequency resolution of 0.0026 Hz. Because of the short duration of the records, the reliability of the spectra is not great. Nonetheless, a broad plateau is present in both spectra between 0.033 Hz and 0.017 Hz. During

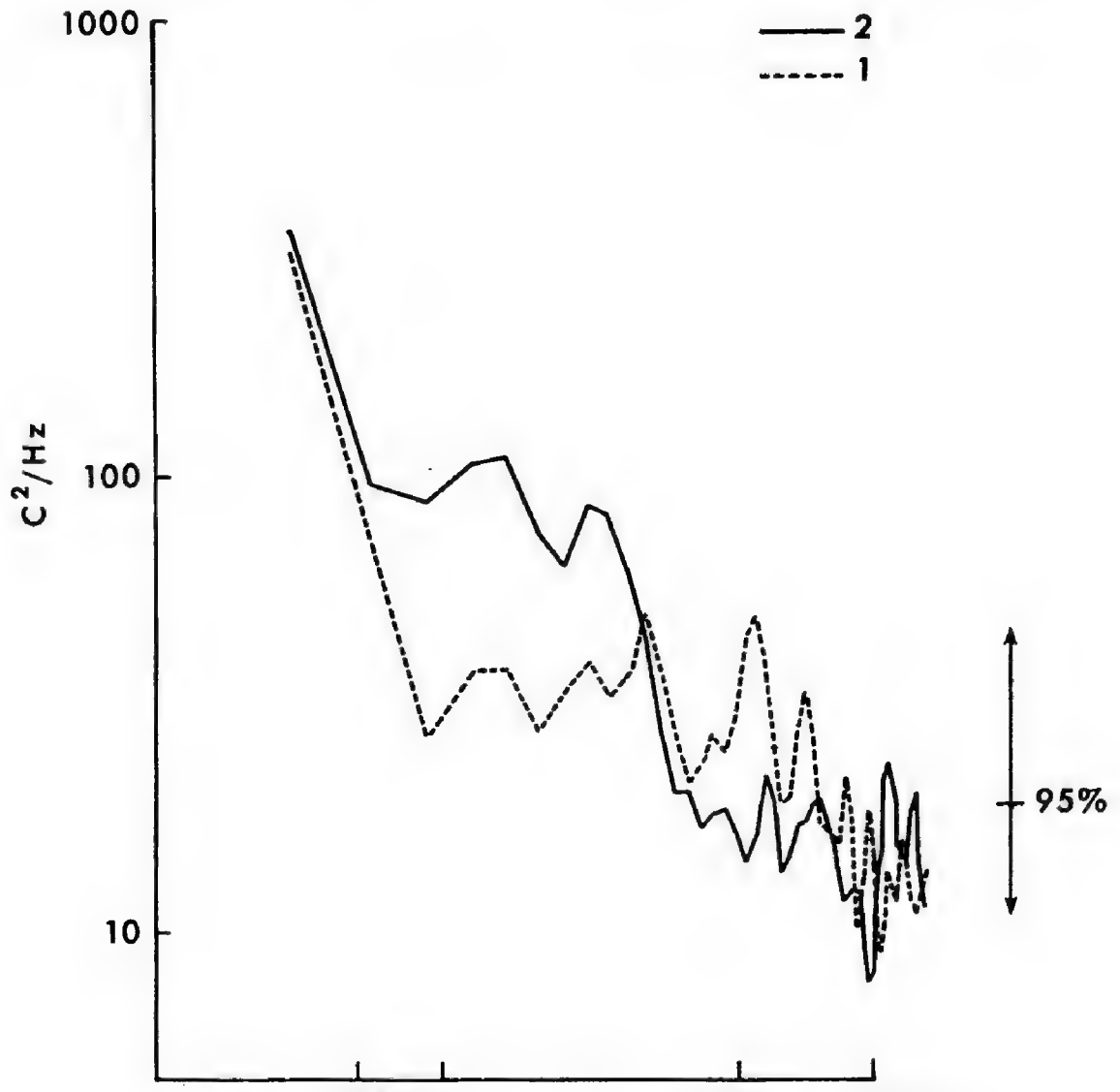

FIG. 15. Spectra from temperature fluctuations measured near the pycnocline outside the South Pass bar. Ninety-five percent confidence intervals are indicated. Thermistors were at the following depths: 1:2 m, 2:2.5 m.

the time of the records, the maximum local Brunt-Väisälä frequency was 0.31 rad sec^{-1}. Peaks in the power spectra are discernible at slightly lower frequencies. Also, at the time of the measurements, packets of long, linear surface "slicks" were observed near the boat. The arrival of a burst of thermal activity could not be identified with the passage of a packet of "slicks," but this may only have been an observational difficulty. The low deck level of our boat made the "slicks" impossible to observe as they passed the thermistor chain. The amplitudes of the thermal fluctuations diminished with time from an initial peak amplitude within any given burst. The records are somewhat reminiscent of those taken by Halpern (1971) in Massachusetts Bay and later modeled analytically by Lee and Beardsley (1974). Interestingly, the 2-m thermistor underwent thermal fluctuations which were composed of a long rise in temperature followed by a rapid drop in temperature. The 2.5-m thermistor variations were a long initial drop followed by a rapid rise in temperature. This pattern is suggestive of a mode II internal wave within the pycnocline region, whereas Halpern's data are readily described by a mode I model. Another difference from Halpern's data is that our

thermal variations increased in amplitude and then rapidly diminished (Fig. 13), while his showed the opposite temporal behavior, yet both recording stations lay downstream of a major topographic feature.

It is difficult to tell from our data whether the borelike pattern seen in the temperature data is due to the nonlinear temperature profile or to a borelike nature of the vertical displacements of the isotherms.

ENTRAINMENT

From the foregoing it seems reasonably apparent that internal waves of various frequencies and wavelengths do commonly occur at the mouth of the Mississippi River. Whether or not these waves can account for the vertical entrainment necessary to maintain the mean circulation observed at this location is an entirely different question. We can obtain some insight through a very simple analysis. At the time that our river mouth data were taken, the surface layer was approximately 3 m thick and was moving with a mean velocity of 0.60 m sec^{-1}. The salt wedge intrusion was not measured at this time, but data taken a few days before suggest an intrusion distance on the order of 6,000 m. At our measurement station, the upper-layer salinity was on the order of 4‰, whereas the lower-layer salinity was 33‰. Thus, a 3-m-thick column of fresh water must have mixed with a 0.36-m-thick column of seawater during its transit over the salt wedge in order to produce the upper-layer water observed at our river mouth anchor station (Fig. 1). This situation implies a mean entrainment velocity over the salt wedge of 3.6×10^{-5} m/sec. Entrainment velocities estimated from Keulegan's formulae (Keulegan 1963) are an order of magnitude greater, but we are not dealing with an arrested saline wedge, as Keulegan assumes, but rather with a salt wedge which responds dramatically to tidal forcing (Wright 1970). During the time it takes the 3-m column of fresh water to traverse the wedge, 400 internal waves of 25-sec mean period are observed at our measurement station. If these waves have an average amplitude of 0.3 m and sinusoidal shape and our data are representative of the situation over the entire wedge, and further assuming that when a wave breaks the entire positively displaced half cycle mixes with the upper layer, then approximately every 40th wave must break to produce the observed situation. If less of the wave form participates in the breaking process, as Keulegan (1949) suggests, then many more waves must "break" in order to produce the observed conditions. This, though, is only an upper estimate on the required breaking; it ignores turbulent mixing and advection from the very turbulent region near the toe of the wedge. Similarly, Wright and Coleman's model of effluent expansion requires an entrainment velocity which, if supplied only by the mass flux caused by breaking internal waves, implies an excessive amount of breaking for the conditions we observed. Turbulent mixing and advection over the river mouth bar crest probably must be incorporated into their model, at least in the immediate vicinity of the bar.

DISCUSSION

The large-scale dynamics near the mouth of a highly stratified estuary have been described in some detail by Cameron and Pritchard (1963) and Wright and his colleagues (e.g., Wright and Coleman 1971). In these discussions, internal waves are invoked as a mechanism for the vertical transport of both mass and momentum, although such waves have not heretofore been observed. Remotely sensed imagery of the mouths of the Mississippi River exhibited many different sorts of periodic structures (Wright *et al.* 1973). These have been attributed to the surface expressions of internal waves. In this paper, we have attempted to summarize these observations and include a description of some measurements of the internal motion of isotherms near South Pass, Mississippi River.

Inspection of the power spectra and coherence estimates and comparison with estimates of the local maximum Brunt-Väisälä frequency suggest that internal waves of high frequency are well developed within both the passes and the effluent from the Mississippi River. Within South Pass, waves of nearly the Brunt-Väisälä frequency were present. The thermal variations were modulated by a long-period fluctuation with a time scale on the order of 10–12 min. A highly coherent motion was also indicated at periods of approximately 1 min.

Over the river mouth bar, a spectrum peak in the temperature records is indicated at periods of 15 sec. This peak can be explained by internal waves only if we have underestimated the intensity of the pycnocline or if the waves were not locally generated but advected into the area from upstream. A well-developed, vertically coherent motion does exist, though, with a time scale on the order of 50 sec, as was observed within the pass.

Outside the bar, but still within the effluent plume, the thermal fluctuations still exhibit coherent motion and periods between 0.5 and 1 min. In this region, the motions are suggestive of a mode II internal wave. These waves are modulated with a time scale on the order of 12–16 min.

The observations just described have not been made synoptically. The remote-sensing imagery was acquired over roughly a 3-year period, and the conventional surface measurements were made during a 1-week period in 1973. Therefore, it is not certain that the same phenomena were being sampled in all cases. The relative stability of the Mississippi River flow regime, the constancy of the density difference between Mississippi River water and coastal water, and the continual recurrence of the same or similar frequencies in all our data strongly suggest such an interpretation of the measurements.

Oscillations with periods on the order of 50–60 sec are present and vertically coherent in all the data sets. These are not the most energetic oscillations, but they do always represent at least a plateau in the energy spectra. The longer period motions (periods on the order of 10–15 min) are also readily apparent in the records from both inside the pass and outside the bar. They may also be present over the bar but were possibly within the noise during our observations. We believe that these long-period motions have as their surface expressions the pulselike phenomena (with surface wavelengths on the order of a few hundred

meters) described above as type I features. Those features described as types III and IV are still unexplained. Within the pass itself, very high frequency internal waves (approaching the Brunt-Väisälä frequency) are also well defined. These waves are possibly partially responsible for the vertical mass transport which maintains the nontidal circulation within the pass. They are not present outside the pass, unless the spectrum peak at periods of 15 sec found over the bar represents the advection of these waves into the bar region.

It has been suggested to us that some aspects of our data, such as the spectrum peak near the Brunt-Väisälä frequency, are very reminiscent of the GM75 model (Garrett and Munk 1975). We feel rather that any resemblances between our data and the GM75 model are purely coincidental. That model was derived for deepwater, isotropic wave fields in an exponential density field. Our data were taken in a shallow-water, nearshore, strongly stratified, and strongly sheared situation which was also definitely anisotropic. In fact, we are unaware of any realistic model for internal waves under the conditions in which our data were collected. As investigations of the inner shelf and nearshore zone continue, the situation will, it is hoped, ameliorate, but presently we are only to the point where we can collect our observations and look for those unifying characteristics which are amenable to fruitful modeling efforts.

We have described observations, which we believe to be unique, of the internal waves at the mouth of a a highly stratified estuary, such as have been hypothesized by numerous investigators of the large-scale dynamics of these river mouths. Some of these waves have been associated with surface phenomena observed on remotely sensed imagery. Other surface features have not yet been explained.

ACKNOWLEDGMENTS

This study was sponsored by the Geography Programs of the Office of Naval Research under Contract N00014–69–A–0211–0007, Project NR 388 002, with the Coastal Studies Institute, Louisiana State University. Many helpful suggestions on the manuscript were made by Drs. David Cacchione and Ned P. Smith. Ms. M. White performed the computer programming. Mrs. G. Dunn provided the illustrations.

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SEASONALITY AND PHYSICO-CHEMICAL RANGES OF BENTHIC MACROPHYTES FROM A NORTH FLORIDA ESTUARY (APALACHEE BAY)

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ABSTRACT

Samples were taken for 15 months in Apalachee Bay, north Florida to determine the seasonality of the various species of benthic macrophytes. A total of 39 species was collected. Quantitatively the flora was dominated by the seagrass, *Thalassia testudinum*, and the green alga, *Halimeda incrassata*. The phylum Rhodophyta had the largest representation with 17 species. The flora was warm temperate with many eurythermal tropical species. One species *Polysiphonia harveyi*, was shown to have a disjunct distribution and a temperate origin.

Environmental limits (temperature, salinity, etc.) for each species were presented. Most species appeared to be eurythermal, which was considered an adaptation of tropical species for existence in a warm temperate region. Both euryhaline and stenohaline species coexist in Apalachee Bay. Species distribution in response to factors such as turbidity, color, and depth was discussed.

INTRODUCTION

Apalachee Bay is located in the northeastern Gulf of Mexico between Alligator Point and Cedar Key, Florida. It is a broad, shallow bay with depths less than 3 m extending approximately 15 km offshore. According to Swanson, *et al.* (1972), this area is one of the least developed portions of the subtropical coast of the United States. Tanner (1960) called this region a "zero energy" coast marked by salt swamps and marshes, drowned karst, open Gulf oyster bars, and slight beach development. No barrier islands exist due to inadequate wave activity and sand. Various small rivers enter the Gulf of Mexico in this region. This survey encompassed the Fenholloway and Econfina River Systems. The specific characteristics of these rivers have been reported by others (Curl 1956, Saville 1966, Gorsline 1966). The Fenholloway drainage has received considerable amounts of kraft mill effluent (KME). This effluent has affected portions of the Gulf of Mexico (Livingston 1975). The KME is composed of a complex mixture of organic acids, polythionates, lignins, sulfides, inorganic substances, etc. When these substances are discharged into the aquatic environment, significant alterations of water quality occur, such as high biochemical oxygen demand, increased color and turbidity, and reduced dissolved oxygen (Zimmerman and Livingston 1976).

Contributions in Marine Science, Vol. 20, 1976.

The benthic macrophytes of Apalachee Bay have been sampled by various investigators. Madsen and Nielson (1950) described some species of algae found at St. Marks, Florida. Humm (1953, 1963) collected seagrasses and marine algae from the vicinity of Alligator Point and St. Marks. Humm and Taylor (1961) sampled marine chlorophytes from this area also. Earle (1969) collected phaeophytes from around the Rock Islands which lie between the Fenholloway and Econfina Rivers. Other than these limited efforts, the benethic macrophytes of Apalachee Bay have not been sampled quantitatively or qualitatively over any extended period of time. During the present 15-month study, qualitative and quantitative samples were collected from the Fenholloway-Econfina region of Apalachee Bay. The purpose of this paper is to describe the seasonality of the individual species of conspicuous benthic macrophytes in terms of presence or absence and standing crop. The effects of certain environmental parameters on individual species are discussed.

MATERIALS AND METHODS

A preliminary diving survey was carried out in offshore areas of the Econfina and Fenholloway river systems. For each drainage system, a series of 7 fixed offshore stations was established (Fig. 1). All stations were identified by permanent markers and/or compass sightings on nearby

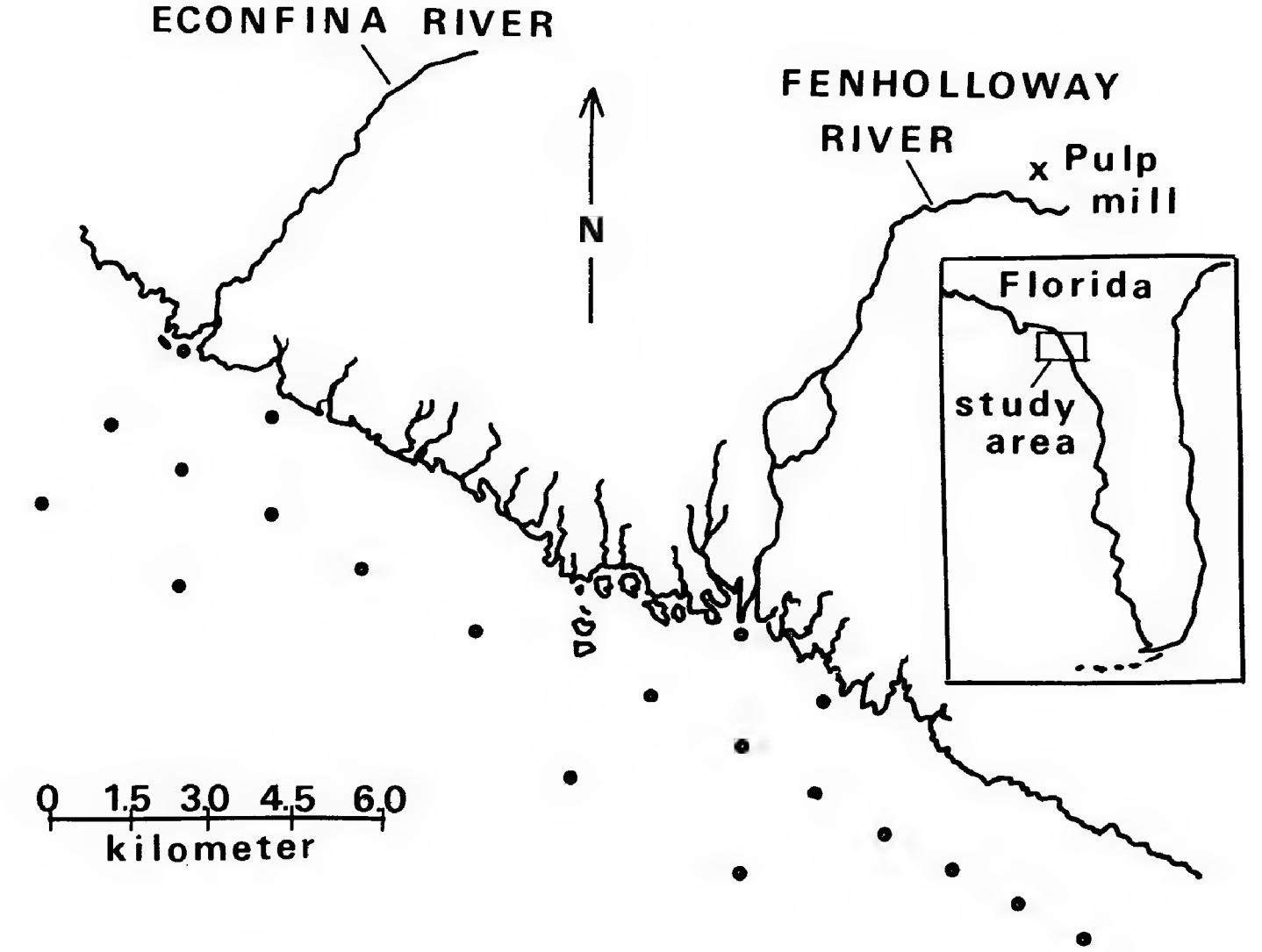

FIG. 1. Drainage area and offshore stations sampled in Apalachee Bay.

landmarks. Water samples (surface and bottom) were taken with a 1 liter Kemmerer bottle. Temperature (C) was measured using a stick thermometer. Salinity was estimated with a temperature-compensated refractometer calibrated periodically with standard sea water. Turbidity and color were measured in order to ascertain the distribution of KME in the offshore waters. Turbidity was measured with a battery operated (Hach) water test kit (Formazin standard method) and a Hach Model 2100-A turbidmeter. Color (total, Pt-Co units) was determined using a Hach APHA platinum-cobalt standard test.

Two methods were used to sample the benthic macrophytes. Qualitative samples were obtained by the use of a 5-m otter trawl. These collections were made from February, 1972 to April, 1973. A representative sample of the benthic macrophytes was taken from each offshore station and returned to the laboratory for identification.

The quantitative benthic samples were made by diving at the 14 stations at monthly intervals from March, 1972 to April, 1973. Samples were taken at each station by throwing a 1 m^2 aluminum hoop from the boat and removing all the benthic macrophytes enclosed by the sampling device. All parts were taken (leaves, stems, rhizomes, roots) and placed (wet) in plastic bags. From March, 1972 to October, 1972, one sample was taken at each station; from November, 1972 to April, 1973, two samples per station were taken. In the laboratory, each sample was washed, sorted according to species, and identified. Rhizomes and roots were separated from shoots and leaves of the seagrasses. Wet weights were made for each portion of the plant. Samples were dried to a constant weight at 105 C. Total dry weights (whole plant) for each species were then determined.

RESULTS

Physico-chemical Factors

A complete analysis of the physical and chemical data has been published (Livingston 1975). Peak water temperatures generally occurred in August and September (31 C) while the lowest temperatures were found in January and February (9 C). There were rapid changes in water temperature during the fall (September–November) and spring (March–May). During the winter, water temperatures were more variable due to periodic cold fronts moving through the area. According to Koenig *et al.*, (1976), the water temperatures in shallow coastal areas of north Florida closely follow the air temperatures. Mean salinity for most stations varied between 20 and 25‰ during the study period, reaching levels of 35‰ at the outermost stations during the fall of the year. Stations of the Fenholloway River system were characterized by higher color levels than comparable areas in the Econfina River system. There were periodic increases in color during winter and spring. Usually, salinity and color had an inverse relationship, implicating land runoff as the source of higher offshore color values. The Fenholloway stations also tended to have higher turbidity values than comparable Econfina stations. The center of Hurricane Agnes struck the northeast Florida coast approximately 100 miles west of Apalachee Bay on June 19, 1972. It had little effect on Apalachee Bay. However, during April, 1973, there was extremely heavy rainfall throughout northern Florida followed by very low salinities and high color values at all stations.

Biological Data

A total of 39 different species of benthic macrophytes was collected. Red algae dominated the list with 17 different species. Table 1 is a listing of each

TABLE I. MONTHLY QUANTITATIVE AND QUALITATIVE RESULTS OF EACH COLLECTED SPECIES (+ - present, blank - absent) (Figures in parentheses - dry weight biomass of that species during that month in grams - March, 1972 to June 1972 and August, 1972 to October, 1972 14 m^2 samples/month; July, 1972 20 m^2 samples/month; November, 1972 and April, 1973 40 m^2 samples/month; December, 1972 to March, 1973 28 m^2 samples/month)

	1972											1973			
	FEB	MAR	APR	MAY	JUNE	JULY	AUG	SEPT	OCT	NOV	DEC	JAN	FEB	MAR	APR
SPERMATOPHYTA															
Halodule wrightii	+	+ (11)	+ (3)	+ (3)	+ (21)	+ (32)	+ (42)	+ (25)	+ (94)	+ (41)	+ (42)	+ (133)	+ (28)	+ (41)	+ (44)
Halophila engelmanni	+	+ (12)	+ (5)	+ (26)	+ (27)	+ (27)	+ (3)	+ (12)	+ (36)	+ (16)	+ (21)	+ (37)	+ (18)	+ (64)	+ (37)
Ruppia maritima	+	+ (2)	+ (1)							+ (338)	+ (1)	+ (3)	+ (2)		+ (1)
Syringodium filiforme	+	+ (176)	+ (221)	+ (170)	+ (330)	+ (551)	+ (643)	+ (394)	+ (468)	+ (189)	+ (144)	+ (339)	+ (330)	+ (54)	+ (211)
Thalassia testudinum	+	+ (866)	+ (408)	+ (1006)	+ (1789)	+ (549)	+ (1172)	+ (1744)	+ (3204)	+ (982)	+ (663)	+ (830)	+ (1518)	+ (1360)	+ (1271)
CHLOROPHYTA															
Anadyomene stellata	+	+ (2)	+ (1)	+ (1)	+ (1)	+ (5)	+ (9)	+ (8)	+ (24)	+ (15)	+ (2)	+ (6)	+ (7)	+ (9)	+ (4)
Caulerpa ashmeadii		+	+			+ (5)	+ (1)	+		+	+	+ (9)	+ (2)	+	+
Caulerpa fastigata									+	+	+				
Caulerpa paspaloides										+	+				
Caulerpa prolifera	+	+ (42)	+ (5)	+ (4)	+ (4)	+ (4)	+ (18)	+ (7)	+ (29)	+ (15)	+ (5)	+ (13)	+ (2)	+ (4)	+ (6)
Chaetomorpha linum															
Cladophora sp.	+	+ (1)	+ (1)	+ (5)	+	+ (22)	+ (4)	+ (2)	+	+	+	+	+ (1)	+	+
Cladophoropsis membranacea															+
Codium isthmocladum	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Halimeda incrassata	+	+ (685)	+ (708)	+ (1238)	+ (2058)	+ (1722)	+ (2230)	+ (2462)	+ (3023)	+ (1174)	+ (227)	+ (1436)	+ (504)	+ (838)	+ (959)
Penicillus capitatus		+ (29)	+ (3)	+ (4)	+ (82)	+ (10)	+ (6)	+ (41)	+ (46)	+ (18)	+ (17)	+ (29)	+ (21)	+ (20)	+ (7)
Udotea conglutinata		+ (2)	+	+ (2)	+		+ (6)	+ (2)	+ (10)		+ (3)		+ (10)	+ (12)	
Udotea flabellum				+ (10)		+ (11)	+ (3)				+	+ (1)	+ (1)		
PHAEOPHYTA															
Dictyota divaricata					+	+	+			+					
Padina vickersiae				+	+	+	+ (7)	+ (8)	+ (29)	+ (6)	+ (1)				
Sargassum filipendula			+ (7)	+	+	+	+		+ (1)	+ (1)					
Sargassum pteropleuron	+	+ (1)	+	+	+ (7)	+ (2)	+ (10)	+ (3)	+ (1)	+ (1)	+	+ (1)	+ (3)	+ (1)	+ (1)
RHODOPHYTA															
Neoagardhiella parvissima			+	+	+	+	+	+	+	+					
Champia parvula														+	
Chondria tenuissima				+	+	+	+	+	+						
Digenia simplex	+	+ (77)	+ (39)	+ (110)	+ (241)	+ (26)	+ (475)	+ (401)	+ (181)	+ (129)	+ (44)	+ (88)	+ (113)	+ (106)	+ (148)
Eucheuma nudum						+	+			+					

Gracilaria cervicornis	+	+ (1)	+ (1)	+ (3)	+ (2)	+ (9)	+ (10)	+ (10)	+ (12)	+ (2)	+ (1)	+ (1)	+ (2)	+ (1)	+ (1)
Gracilaria foliifera	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Gracilaria verrucosa	+	+ (1)	+ (1)	+ (1)	+ (2)	+ (1)	+ (6)	+ (8)	+ (24)	+ (15)	+ (2)	+ (6)	+ (7)	+ (9)	+ (4)
Halymenia floridana					+	+	+								
Halymenia floresia				+	+	+	+	+	+						
Jania pumila	+											+	+	+	
Laurencia intricata	+	+ (1)	+ (1)	+ (1)	+ (1)	+ (1)	+ (1)	+ (1)	+ (1)	+ (1)	+ (1)	+ (2)	+ (3)	+ (5)	+ (1)
Laurencia papillosa															
Laurencia poitei	+	+ (54)	+ (23)	+ (10)	+ (60)	+ (12)	+ (91)	+ (26)	+ (63)	+ (29)	+ (11)	+ (16)	+ (25)	+ (23)	+ (5)
Polysiphonia harveyi	+	+ (1)	+							+ (4)	+ (1)	+ (12)	+ (48)	+ (161)	+ (49)
Polysiphonia subtilissima					+	+	+	+							
Spyridia filamentosa	+	+	+							+		+	+ (19)	+ (42)	+ (1)
TOTAL NUMBER OF SPECIES PER MONTH	20	21	23	23	25	27	27	23	24	28	24	22	23	22	24

TABLE 1 corrections:

Chaetomorpha linum	1972, Aug. (+)
Gracilaria foliifera	1973, Jan. (blank)
Laurencia papillosa	1973, Apr. (1)

species taken by month in qualitative and quantitative collections. Table 2 summarizes the physico-chemical ranges of all the species collected. The extreme low salinities and high color values that occurred in April, 1973 have been put in brackets because of their unusual nature and unknown effects.

DISCUSSION AND CONCLUSIONS

Number of Species

The total number of benthic macrophyte species is low. Edwards and Kapraun (1973) collected 89 species of algae in the vicinity of the University of Texas Marine Science Institute at Port Aransas, Texas over a 26 month period. Kapraun (1974) collected 31 new species of algae along the Louisiana coast. Combining this with the previously published investigations resulted in a list of 85 species for the Louisiana Gulf coast (Kapraun 1974). Phillips (1960) collected 165 species of algae (exclusive of cyanophytes) in the vicinity of Tampa Bay, Florida.

The low species number of this study is due to two factors. The nearshore seagrass beds were the only areas extensively studied. The limestone outcroppings, wooden pilings, oyster reefs and salt marshes were not sampled. Earle (1969) regarded the limestone outcroppings to be the mist significant feature with regard to algal distribution in Apalachee Bay. We are convinced that a thorough study

TABLE 2. PHYSICO - CHEMICAL RANGES OF EACH COLLECTED SPECIES (Figures in parentheses - uncharacteristic values from April, 1973)

Species	Habitat E-Epiphyte, A-Attached, D-Drift	Salinity ‰	Temperature °C	Color Pt-Co Units	Turbidity (STU)	Depth (m)
Spermatophyta						
Halodule wrightii	A	17(6)-36	9-31	0-200(270)	0-55	0.8-3.0
Halophila engelmanni	A	17(11)-36	9-30	0-200(270)	0-55	0.8-3.0
Ruppia maritima	A	16-24	12-21	10-190	0-55	0.9-1.3
Syringodium filiforme	A	17(6)-36	9-31	0-180(300)	0-55(60)	0.8-3.0
Thalassia testudinum	A	17(6)-36	9-31	0-180(300)	0-55(60)	0.8-3.0
Chlorophyta						
Anadyomene stellata	D	16(6)-34	11.5-29	0-120(300)	0-30	1.0-2.8
Caulerpa ashmeadii	A	19(6)-31	9-30	0-160	10-50	0.9-2.5
Caulerpa fastigata	A	24-36	14-24	10-110	0-50	1.1-2.3
Caulerpa paspaloides	A	16-31	21-27	0-140	0-15	1.3-2.8
Caulerpa prolifera	A	17(6)-36	9-30	0-200(300)	0-50	0.8-3.0
Chaetomorpha linum	D	25	29	0	0	1.5
Cladophora sp.	D + E	17-33	9-30	0-200	0-55	0.9-2.3
Cladophoropsis membranacea	D + E	32(6)-34	20-31	35-60(140)	0-10	1.1-2.3
Codium isthmocladum	D + A	20-29	13-31	10-40(180)	20-30	1.6-2.0
Halimeda incrassata	A	17(6)-36	9-31	0-170(300)	0-60	.8-3.0
Penicillus capitatus	A	16-36	9-30	0-140	0-40	1.3-3.0
Udotea conglutinata	A	17-35	9-26.5	20-200	0-25	1.3-2.5
Udotea flabellum	A	20-33	11.5-28	15-40	0-10	1.2-2.0
Phaeophyta						
Dictyota divaricata	D + A	27-31	27-30	10-40	10-20	1.3-2.5
Padina vickersiae	E + A	19-31	13-31	0-60	0-25	1.3-2.5
Sargassum filipendula	A	25-35	25-31	0-30	0-15	1.3-2.3
Sargassum pteropleuron	D + A	12-33	9-31	0-200	0-40	0.8-23
Rhodophyta						
Neoagardhiella ramosissima	D	22-36	13-31	0-40	0-50	1.3-3.0
Champia parvula	D	21-25	17	140-170	21-25	1.0-1.5
Chondria tenuissima	D	12(17)-30	12-28	0-140(200)	0-10	0.9-2.8
Digenia simplex	E + D + A	17(6)-36	9-31	0-170(300)	0-50(60)	0.9-3.0
Eucheuma nudum	D + A	28	15	40-50	30	1.6-2.0
Gracilaria cervicornis	D + A	12-33	9-31	0-310	0-80	0.5-2.3
Gracilaria foliifera	D + A	16-30	9-31	0-190	0-90	0.9-2.0
Gracilaria verrucosa	D + A	12(6)-33	9-31	0-405	0-110	0.5-2.8
Halymenia floridana	D	24-33	24-30	0-15	0-30	2.0-2.8
Halymenia floresia	D	21-33	19.5-28	0-50	0-38	2.0-3.0
Jania pumila	E	17(12)-23	11.5-21	0-50(300)	0-30	0.9-1.5
Laurencia intricata	E + D + A	16-33	9-30	5-140	0-25	0.9-3.0
Laurencia papillosa	D	19	20	14	0-90	1.5
Laurencia poitei	E + D + A	17(6)-36	9-31	0-405	0-110	0.8-3.0
Polysiphonia harveyi	E + D	16(6)-28	12-20	0-170(300)	0-20(55)	1.0-2.3
Polysiphonia subtilissima	D	14	18	120	0	1.5
Spyridia filamentosa	E + D	16-31	9-22	15-140	0-30	.9-2.5

TABLE 2 correction:

Sargassum pteropleuron Depth (m), 0.8–2.3

of these other habitats would yield many more species. In addition, the method of selecting the macroalgae contributed to the results. Only algae that were approximately 1 cm long or comprised conspicuous tufts were identified. Many small epibenthic and encrusting algae were not sought out, identified, or reported. Thus, this study was relegated to certain dominant microhabitats in the shallow portions of the northern Gulf, and was not intended to be a synoptic survey of the entire flora.

Seasonal Distribution and Floristic Affinity

According to the Stephensons (1952), a warm temperate region is characterized by minimum winter sea temperatures of 10 and 20 C and summer maxima near 25 C. Apalachee Bay fits this description fairly closely. The range is somewhat expanded here due to the shallowness of the area. Taylor (1955) believed that the flora of the northern Gulf of Mexico was generally impoverished and rather undiversified. He believed it was the eurythermal remains of the previous tropical Caribbean flora. Conover (1964), Edwards and Kapraun (1973), and Kapraun (1974) found a rather diverse flora with temperate elements along the Texas and Louisiana Gulf of Mexico coasts.

Most of the species that were found in Apalachee Bay have tropical affinities. Many existed throughout the year but showed distinct seasonal variation in biomass. This group includes many of the dominant species such as *Thalassia testudinum*, *Halimeda incrassata*, *Syringodium filiforme*, *Digenia simplex*, and *Laurencia poitei*. Others tended to have patchy distributions causing many irregularities in their biomass over time. However, they were all present throughout the year. This list included *Halophila engelmanni*, *Caulerpa prolifera*, *Anadyomene stellata*, *Penicillus capitatus*, *Laurencia intricata* and species of *Udotea* and *Gracilaria*. One seagrass, *Halodule wrightii*, had a very patchy distribution; this species is noted for its eurythermal characteristics. It has been collected from Beaufort, North Carolina while the other seagrasses' northern limit is Cape Canaveral, Florida (Phillips 1960).

Four members of the order Siphonales were abundant in the sampling area. These were *Halimeda incrassata*, *Penicillus capitatus*, *Udotea conglutinata* and *Udotea flabellum*. Humm and Taylor (1961) stated that these species should have a continuous Florida distribution from the Florida Keys to Pensacola. These species have not been found in a series of studies in an area west of Apalachee Bay (William Roth and Henry Bittaker, personal communication). Edwards and Kapraun (1973) and Kapraun (1974) did not report the presence of these species along the Texas and Louisiana coasts. It is quite possible that Apalachee Bay represents the northern limit of these species, and they may be entirely absent along the remaining northern Gulf coast.

There were some species which appeared only during warmer months of the year. These either died or entered an unknown resting stage after the water temperature dropped. All the brown algae exhibited this type of seasonality. *Dictyota divaricata* appeared in early spring on limestone outcroppings where it flourished until the fall. *Padina vickersiae* was most often found attached to

Digenia simplex. Plants of this species observed during the late fall or early winter had a deformed and ragged appearance. Earle (1969) found that these two species were annuals. Species of *Sargassum* were first collected during the late spring, often attached to oyster shells or limestone outcroppings. By early fall some plants were observed to be greater than 1 m in length. After the initial temperature drop, these were often broken up and were present as drift. Earle (1969) believed that these species were perennials which died back to their holdfast during the winter and then regenerated in the spring. One species, *S. filipendula*, is present as far north as Massachusetts (Taylor 1957). However, the genus *Sargassum* is considered to be tropical.

Some red algae were also collected only during warm months. This group consisted of *Neoagardhiella ramosissima*, *Eucheuma nudum*, *Halymenia floresia* and *H. floridana*. None of these species were observed to be attached but were found as drift material. According to Humm (1973), these genera are stenohaline and more or less restricted to the open Gulf or waters of highly stable salinity. Therefore, it is highly likely that these algae grew in deeper waters in Apalachee Bay, were detached by wave action, and then moved into the study area.

Three species of red algae were more abundant during the winter months. These were *Jania pumila*, *Polysiphonia harveyi*, and *Spyridia filamentosa*. All three species appeared during the early winter and disappeared in early spring. Humm (1964) had reported the occurrence of *Polysiphonia harveyi* from Alligator Harbor, Florida, approximately 30 miles west of Apalachee Bay. According to Taylor (1957), this species is commonly found from South Carolina to Nova Scotia, and is not found in south Florida (Mathieson and Dawes 1975). Edwards and Kapraun (1973) found 8 disjunct species along the Texas Gulf coast of temperate North Atlantic affinity during winter and spring. We believe that *P. harveyi* is also such a species. *Spyridia filamentosa* has a wide distribution from the Caribbean to southern Massachusetts (Taylor 1957). There were other algae that also had a wide distribution such as *Chaetomorpha linum*, *Champia parvula*, *Chondria tenuissima*, *Gracilaria foliifera*, *G. verrucosa*, and *Polysiphonia subtilissima*. These have been found in southern New England (Taylor 1957). One angiosperm, *Ruppia maritima*, was observed throughout the year but was collected most often during the late fall and winter. This species is distributed from Maine to the Florida Keys (Phillips 1960).

Range of Physico-chemical Factors for Benthic Macrophytes of Apalachee Bay

The limiting chemical and physical factors of most benthic macrophytes have been extensively studied. A co-dominant in Apalachee Bay, *Thalassia testudinum*, has been studied extensively by Phillips (1960). Our results coincide closely with his. However, the winter minimum temperature of 9 C was approximately 3 C less than that reported by Phillips (1960). There was a major leaf kill of *T. testudinum* in November when water temperatures dropped below 15 C. Phillips (personal communication) observed that the blades died back to the

rhizome. However, in Apalachee Bay, very short green shoots remained throughout the winter even when water temperatures were under 10 C. This could be a physiologically adapted population of *T. testudinum* which is more tolerant to low temperatures. Some defoliation was observed in later summer when water temperatures reached 30 C. This was also the time of the year of the highest salinities, 36‰, and highest standing crop (Zimmerman and Livingston 1976). However, according to Moore (1963), this was within the optimum range for *T. testudinum*. The lowest salinity observed was 6‰ in April, 1973; since no further samples were taken, the effects of such low salinity are not known. Phillips (1960) did observe *T. testudinum* in water of 10‰ after a summer shower. Most stands of *T. testudinum* existed in waters with salinities greater than 20‰ but it can withstand lower salinities for short periods of time. In Apalachee Bay the low salinities occurred in late winter and early spring when temperatures were not yet optimum. According to Moore (1963), *T. testudinum* requires considerable sunlight; if high color and turbidity values persist over a long period of time, this could destroy *T. testudinum* beds. In Apalachee Bay the high turbidity and color values generally occurred in later winter and early spring. In late spring Apalachee Bay warmed and cleared up coinciding with rapid growth. Therefore, Apalachee Bay was unfavorable to such growth of *T. testudinum* during late winter and early spring. Zimmerman and Livingston (1976) believed that *Thalassia* biomass was much reduced in the Fenholloway drainage because of high color and turbidity values. The depth at which *T. testudinum* existed in Apalachee Bay was well within ranges previously reported by Humm (1956), Phillips (1960), and Moore (1963). No reproductive structures or seedlings of *T. testudinum* were ever observed during this study. It seems that this area is the northern limit of this species in Florida and it might rarely or never reproduce sexually in Apalachee Bay.

Syringodium filiforme was found in abundance in the study area. The range of temperatures, salinities, turbidities, and color for the other seagrasses (except *Ruppia maritima*) was almost identical to that of *Thalassia testudinum*. This distribution could be an oversimplification since *S. filiforme* was more plentiful in areas in which *T. testudinum* was not dominant. Zimmerman and Livingston (1976) reported more *S. filiforme* than *T. testudinum* in the polluted Fenholloway River system. This species also was found in the shallower, less saline waters immediately offshore of the Econfina River. There was also some leaf kill during the winter months. However, it was not as extensive as the *T. testudinum* leaf kill, and many leaves still remained attached to the rhizomes. From this study it seems that *S. filiforme* tolerates longer periods of low salinities, lower temperatures, and higher turbidity and color values than *T. testudinum*. Phillips (1960) also found that *S. filiforme* existed in areas of low salinity where *T. testudinum* was not present. McMillan and Moseley (1967) found that *S. filiforme* was less tolerant of high salinities than the other seagrasses. Since the salinities of this study area were much lower than those used in his laboratory work, no real comparisons could be made. Phillips (1960) reported that flower-

ing *S. filiforme* plants were rare in the Tampa area. A number of flowering *S. filiforme* plants were collected in the quantitative meter square samples in May and June, 1972 (water temperature, 26 C; salinity, 28‰).

The seagrasses *Halodule wrightii* and *Halophila engelmanni* were very similar to the other species in their physico-chemical ranges. However, their distribution in Apalachee Bay was very different from the other two seagrasses. There was little leaf kill of *H. wrightii* during the winter months, further indicating the eurythermal nature of this species. Phillips (1960) reported a low temperature of 13.3 C for *H. engelmanni*. The 9 C reported here is a new minimum for this species. Both species are euryhaline. *Halodule wrightii* was known to exist in salinities from 1‰ to 60‰ (Simmons 1957). According to Humm (1973), *H. engelmanni* does not tolerate much reduction in salinity and is, therefore, restricted to higher salinities. A bed of *H. engelmanni* was observed at the mouth of the Econfina River, an area with generally low salinities. In 1970, den Hartog reported this species in water of 11‰. Therefore, it seems that *H. engelmanni* is definitely euryhaline. Both of these species had higher biomass in the Fenholloway region than the Econfina region. They were able to exist in areas with significantly higher turbidity and color values. *Halophila engelmanni* is known to exist in water as deep as 90 m (Taylor 1928); therefore it is not unexpected that it would flourish in the lower light intensities in the offshore area of the Fenholloway River. *Halodule wrightii* generally appears higher in the intertidal zone than any species of seagrass. It can grow in deeper water also, but is generally out-competed by *Thalassia testudinum* and *Syringodium filiforme* in such areas (Humm 1973). The abundance of *H. wrightii* in the Fenholloway region may be correlated with the lower light intensities and/or the reduced abundance of *T. testudinum* and *S. filiforme* (Zimmerman and Livingston 1976). No flowers were observed for either species; however, Phillips, *et al.* (1974) have recently found flowering material in Redfish Bay, Texas which is along the northwest coast of the Gulf of Mexico. *Halodule wrightii* and *H. engelmanni* seem to be the most tolerant of varying environmental conditions of any of the seagrasses found in the Gulf of Mexico.

According to Humm (1973). *Ruppia maritima* is a freshwater grass-like plant that may invade brackish water and areas of higher salinity. Phillips (1960) found this species in Tampa Bay in water of less than 25‰ salinity and temperatures ranging from 7 C to 35 C which corresponded well with our findings. He also noted that *R. maritima* occurred in areas of poor light penetration. In Apalachee Bay it was found exclusively near the mouth of the Econfina River, an area with wide variations of salinity and turbidity. This species was not found in the Fenholloway drainage, so there may be limits to the degree of color and turbidity it can tolerate. During May and June, numerous flowering plants were observed, an indication that good conditions existed for the reproduction of *R. maritima*. The water temperature was 27 C and the salinity was 24‰, which corresponds well with McMillan and Moseley (1967) who found that this species would not flower in salinities over 30‰.

Much is known about the ranges of environmental factors which influence the distribution of various species of algae. Humm (1973) indicated that members of a number of genera were generally stenohaline and, therefore, restricted to the open Gulf of Mexico. This list included the red algae of the genera *Eucheuma*, and *Halymenia*, and the green algae of the genera *Caulerpa*, *Udotea*, *Penicillus*, *Halimeda*, and *Codium*. Another group were the euryhaline genera which colonized estuaries and inshore areas subject to periodic salinity fluctuations. The salinity fluctuations were due to variation in land runoff which also caused fluctuations in the color and turbidity of areas near the river mouths. Genera in this group consisted of *Jania*, *Neoagardhiella*, *Spyridia*, *Digenia*, *Gracilaria*, *Polysiphonia*, *Chondria*, and *Laurencia*. Generally the algae from Apalachee Bay fit this scheme. The green algae (*Halimeda*, *Caulerpa*, etc.) were found at the outer stations while red algae such as *Digenia*, *Laurencia*, and *Gracilaria* occurred at both inner and outer stations. *Neoagardhiella ramosissima* was found exclusively at outer stations as drift material and, therefore, should be included with the other stenohaline species. Of the brown algae, *Sargassum pteropleuron* was the most tolerant of varying environmental parameters. It belongs to the euryhaline group, while the other brown algae were typically stenohaline. *Padina vickersiae* was generally found as an epiphyte on *Digenia simplex*, but only during the summer when salinities were high and color and turbidity values were low.

These ranges have to be observed with a certain amount of caution. Many of these plants must be able to tolerate adverse conditions for at least a short period of time or die. The optimum conditions for many of these species are within the ranges of the environmental factors given in this paper. However much more laboratory and field work must be done concerning agents which determine the distribution of benthic macrophytes. This is especially true of the five species of seagrasses. Factors such as sediment type, nutrients, pollutants, and competition should be included in such studies.

ACKNOWLEDGMENTS

The authors wish to thank Drs. Clinton J. Dawes, E. I. Friedmann, and William Roth for their help in identifying some of the species in the more difficult genera of benthic algae. Special thanks also to Henry F. Bittaker for reviewing the text and his helpful criticism. We also wish to acknowledge the fine and very helpful reviews given by Drs. Peter Edwards and Ronald C. Phillips. We are also deeply indebted to Mr. J. H. Millican and Buckeye Cellulose Corporation for their financial support during the writing of this article.

The collection of these data was supported by a grant from the Coastal Coordinating Council of Florida.

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GEOGRAPHIC VARIATIONS IN SALT MARSH MACROPHYTE PRODUCTION: A REVIEW

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ABSTRACT

A review of salt marsh macrophyte production measurements supports the conclusion of a north-south gradient which parallels solar energy inputs at a 0.20–0.35% net conversion efficiency. There is considerable variation within and among marshes. Methods previously employed to measure salt marsh macrophyte production have generally underestimated the actual net aboveground production because of an inability to account for the turnover of live material between sampling periods. Turnover apparently increases with decreasing latitude and may be equal to annual changes in standing live biomass. The effect of other factors influencing production are discussed and a detailed data review presented.

INTRODUCTION

Several theories and observations on the causes of variation in salt marsh production have been put forward. This paper represents an attempt to review the literature on salt marsh macrophyte production, especially for *Spartina alterniflora*, and to present a framework for comparisons of salt marsh production studies in terms of 1) methods; 2) regional variations; 3) local variations; and 4) the net solar energy conversion efficiency.

Such an effort was thought desirable, in part, because an extensive data set is now available on the production of large monotypic plant populations which are found over a wide geographical range.

Until recently, there were only a half-dozen papers on salt marsh macrophyte annual production. Additions to these data have been accompanied by observations on the changes in production with latitude. Latitudinal gradients have been reported by Stroud and Cooper (1968), Woodwell, *et al.* (1972), Williams (1972) and Keefe (1972), but these reports included a maximum of only 10 locations. Tidal amplitude has been suggested as a significant influence by Steever (1972), and the importance of tidal energy has been indirectly promoted by others (e.g. Schelske and Odum 1961, Odum and Fanning 1973). Mann (1972) and Hatcher and Mann (1975) have suggested that Canadian marshes are more productive than many southern ones. Gabriel and de la Cruz (1974), and de la Cruz (1973) suggested that marsh production of both monotypic and pure stands are nearly similar regardless of location. One serious complicating

factor is that most summaries to date have mixed results from the various methods used to measure productivity of salt marsh macrophytes.

R. G. Wiegert has stressed the necessity of using techniques capable of estimating the turnover rate of plant material in terrestrial grasslands (i.e., Wiegert and McGinnis 1975; Wiegert and Evans 1964). He has pointed out how standing biomass sampling inadequately estimates total annual plant production. There are now enough data to examine how the techniques presently used in salt marshes compare with each other over a wide geographical range and to examine relative turnover rates in salt marshes.

METHODS

The literature was reviewed of all the known original publications concerning production of monotypic stands of *S. alterniflora*. The sampling locations cover most of the Atlantic and Gulf coastal marshes (Fig. 1). Conflicts with quotations of the data in later reports were resolved by obtaining the original reports. Some data were taken from graphs and this introduced errors. Occasional errors in the original tables were corrected when found. All data were converted to dry weight per m^2 of marsh surface, exclusive of the area of tidal creeks, estuaries, and mud flats. If the original report did not include an estimate of annual production using any of three methods, it was calculated when possible. These methods were:

1. *End of the season* estimates of live (EOSL), dead (EOSD), and total (EOST) biomass.

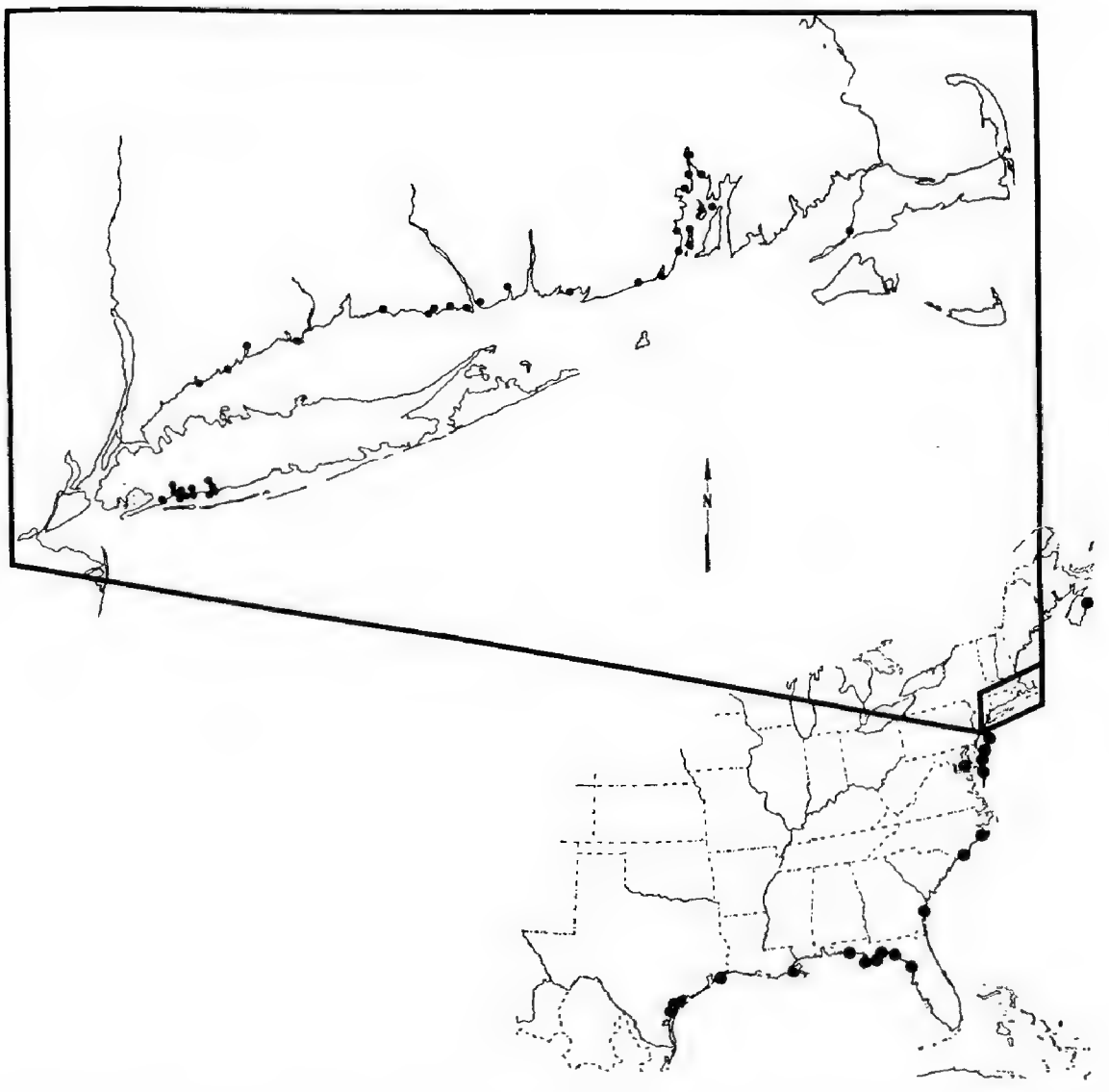

FIG. 1. Locations of sites sampled to estimate *Spartina alterniflora* annual production.

2. *Max-min* or the maximum amount of live material at the "peak" of the growing season less the seasonal minimum standing crop of live material.

3. *Smalley's*. This method, as outlined in Smalley (1958), is an attempt to account for the turnover of particulate material during the growing season due to the death of live plants, herbivory, and removal of material from the marsh by other factors. Annual production is assumed to be the sum of the production between sampling intervals which is calculated as follows: 1) if the net change between sampling periods is positive for both the live (L) and the dead (D) material, then production is equal to the sum ($\Delta L + \Delta D$); if ΔL and ΔD are negative, production is assumed to be zero; 3) if ΔL and ΔD are $+$ and $-$, respectively, then production is equal to ΔL; and 4) if ΔL and ΔD are $-$ and $+$, respectively, production is assumed to be equal to the sum ($\Delta L + \Delta D$) if the sum is greater than zero, and equal to zero if the sum is negative.

Other methods have been used to estimate leaf losses from live plants (Williams and Murdoch 1969, Odum and Fanning 1973, Hatcher and Mann 1975). Kirby (1972) estimated the turnover of dead material with a litter bag methods and used this estimate together with changes in live and dead biomass to calculate net production. Young (1974) used a modification of Smalley's method and Reimold, Gallagher, Linthurst and Pfeiffer (1975) employed Wiegert and Evan's (1964) paired-plot method.

Several published reports were not included in the final comparative analysis of production estimates. This was because the data were unavailable, because live material was not separated from the dead material, or because averages were reported for a particular marsh type and not for all the marsh or were not averaged for the entire marsh. Good's (1965) data were excluded because of the early sampling date (July 5) and Johnson's (1970) because 1) the marsh sampled was dominated by both *S. alterniflora* and *Peltandra virginica*, and 2) the sampling transects ran parallel to a creek.

Marshall's (1970) data were converted to a marsh average by assuming that the percentage of streamside and inland marsh was similar to that of Williams and Murdoch (1969). Morgan's (1961) data for a *S. alterniflora*-dominated marsh were recalculated to that of a monotypic stand by eliminating sites with mixed vegetation from the original data. Estimates of macrophyte production for salt marshes dominated by macrophytes other than *S. alterniflora* were collected in a similar manner.

Tide data were obtained from the original reports, companion research papers, or tide tables (Tide Tables, 1973) for the nearest locations.

Data on the growth response of plants to experimental treatments are included to complete the review but were not used in the graphic presentations.

RESULTS AND DISCUSSION

Methods Comparison

A comparison of results from different methods used to measure annual aboveground production for *S. alterniflora* is shown in Figure 2. The data were derived from Tables 1 and 2, as were several other analyses which follow. The max-min method was consistently the lowest estimator of annual production, as expected. The results by Smalley's method appeared to be curvilinearly related to the lower EOSL estimates; that is, the divergence increased with higher EOSL. Other methods gave the highest results since they, in general, attempt to correct for losses occurring between sampling periods.

Some notes on Smalley's method need to be made here. As long as the live biomass is increasing between sampling periods, the errors in the estimates of the actual amount of live material may be corrected in the succeeding sampling period. An underestimate one month may be compensated for by an overestimate

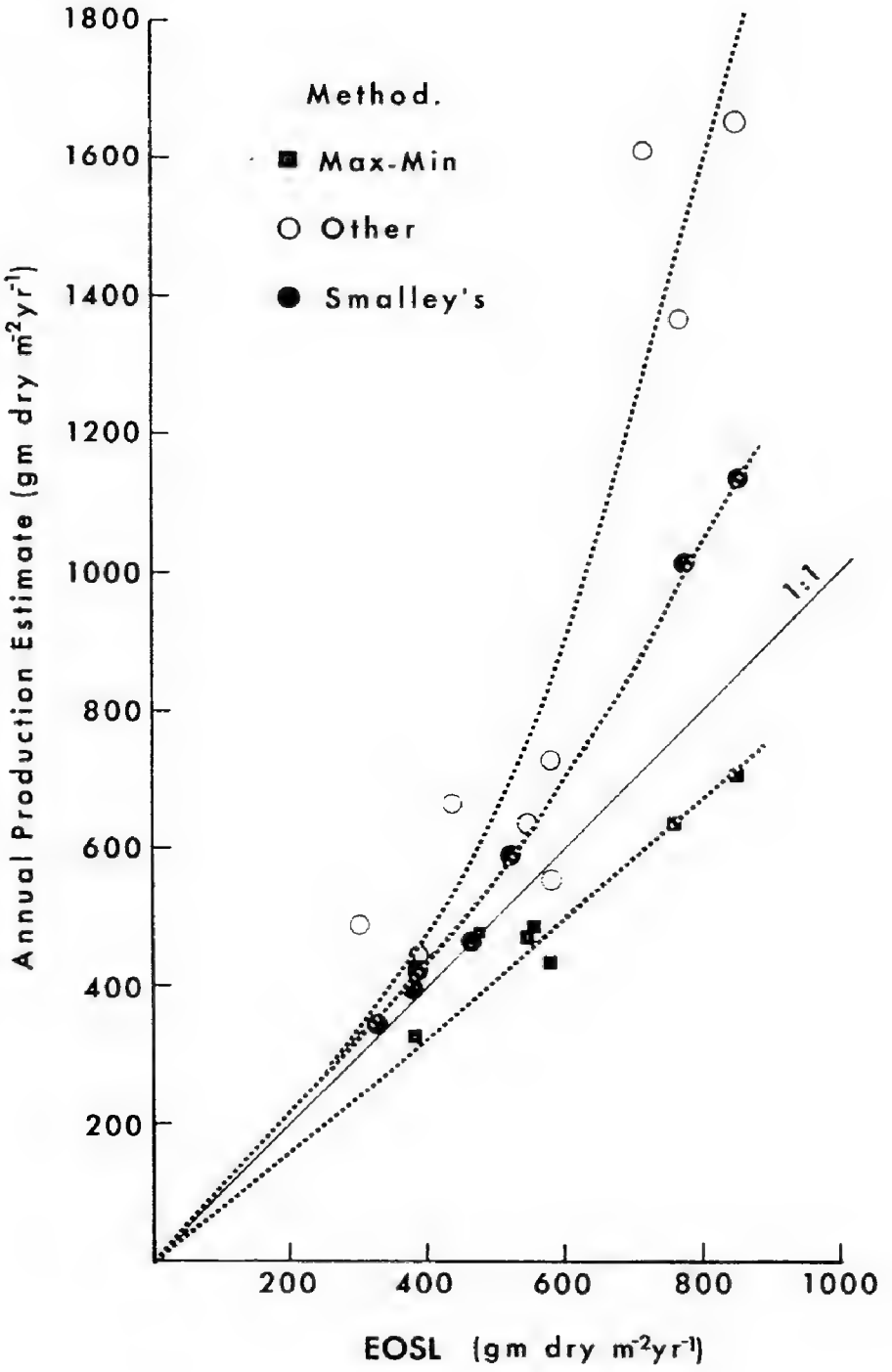

FIG. 2. A comparison of marsh average end-of-the-season live (EOSL) estimates with other methods used to estimate annual production of *S. alterniflora*. Curves fit by eye.

the next month. On the average the total sum of the estimates of production during the growing season approaches the actual production and is closest when death between sampling periods is lowest. When live biomass is declining however, errors accumulate. Negative net production is considered a contradiction in terms and though measured is disregarded for that sampling period. However, the errors in the estimate of the actual amounts of live and dead material present are carried forward and are not (and cannot be) corrected for. This is illustrated in the following example. If the actual amounts of live and dead material are 1000 and 600 g dry wt m^{-2}, respectively, at time t=1, and then 900 g and 700 g at t=2, it is possible within the limits of experimental error to measure these at

TABLE 1

Annual *Spartina alterniflora* above-ground production (g dry wt m^{-2})

Location	Latitude	Tidal Amplitude (m)	Marsh Type	Live (FOSL)	Dead (FOSD)	Total (FOST)	Ratio Live:Dead	Max-Min Method	Z FOSL	Smalley's Method	Z FOSL	Year	Source
Louisiana	29°30'	.30	Streamside	1018	942	1960	1.1:1	752	.74	1409	1.38	2645	Firby, 1972
			Inland	782	757	1544	1.0:1	700	.89	1005	1.28	1323	
			Marsh average	845	784	1629	1.1:1	712	.84	1138	1.35	1647	
Louisiana	29°30'	.30	Streamside:										Allen, 1974
			Control	1056	888	1944	1.2:1	-	-	-	-	-	
			Experimental 1	732	758	1490	1.0:1	-	-	-	-	-	
			(dredging sites; 2	452	454	906	1.0:1		-	-	-	-	
			oil fields) 3	639	661	1961	1.0:1		-	-	-	-	
Louisiana	29°30'	.30	200 m transects perpendicular to streamside:										Gosselink, Hopkinson & Parrando, 1975
			W. Terrebonne Bay	532	669	1201							
			E. Terrebonne Bay	394	624	1018							
			W. Barataria Bay	798	980	1778							
			E. Barataria Bay	650	761	1441							
			Average	594	758	1352	0.78:1	-	-	-	-	-	
Mississippi	29°30'	.3	Tall	1473	-	-	-	-	-	1964	1.33	-	De la Cruz, 1974 (pers. comm.)
			Short	-	-	-	-	-	-	1064	-	-	
Texas	27°50'	.30	Marsh average	428	253	735	1.9:1	-	-	-	-	-	Turner & Gosselink, 1975
	28°10'	.30	"	938	613	1551	1.2:1	-	-	-	-	-	
	28°10'	.30	"	735	408	1143	1.8:1	-	-	-	-	-	
	29°20'	.58	"	923	923	1846	1.0:1	-	-	-	-	-	
Florida	29°50'	1.04	"	772	429	1201	1.8:1	-	-	-	-	-	
	29°50'	1.04	"	593	-	-	-	-	-	-	-	-	
	30°00'	1.04	"	824	457	1281	1.8:1	-	-	-	-	-	
	29°50'	1.04	"	617	-	-	-	-	-	-	-	-	
Florida	28°50'	.76	Marsh average:										Young, 1974 (pers. comm.)
			Control	580	-	-	-	-	-	-	-	-	
			Feb-June	-	-	-	-	-	-	-	-	281	
			+ heat	580	348	721	1.7:1	436	.75	-	552	-	
Georgia	31°20'	2.07	Optimum site:										Odum & Fanning, 1973
			Streamside	3018	297	3315	10.2:1	-	-	-	-	3990	
			High marsh	2018	164	2182	12.3:1	-	-	-	-	2362	
			Marsh average	2335	206	2544	11.3:1	-	-	-	-	2883	
Georgia	31°20'	2.07	Streamside	1230	0	1230	∞ :1	1098	.89	1098	.89	2240	Smalley, 1958
			High marsh	472	275	747	1.7:1	354	.75	643	1.36	643	
			Marsh average	762	143	905	5.3:1	645	.85	1010	1.15	1364	
Georgia	31°20'	2.07	Infrared imagery:										Gallagher et al., 1972
			Red	1665	301	1966	5.5:1	-	-	-	-	-	
			Light-red	630	169	799	3.7:1	-	-	-	-	-	
			Blue-red	499	226	725	2.2:1	-	-	-	-	-	
			Blue	331	57	388	5.8:1	-	-	-	-	-	
			Marsh average	781	188	969	4.2:1	-	-	-	-	-	
Georgia	31°21'	2.07	Tall	1300	-	-	-	-	-	-	-	2375	Reimold et al., 1975
			Short	310	-	-	-	-	-	-	-	1363	
			Marsh average	568	-	-	-	-	-	-	-	1627	
North Carolina	34°00'	1.43	Short	259	196	455	1.3:1	223	.86	329	1.27	279	Stroud & Cooper, 1968
			Medium	477	409	885	1.2:1	415	.87	461	.97	471	
			Tall	1319	433	1752	3.0:1	1170	.89	1296	.98	1563	
			Marsh average	398	192	573	1.9:1	335	.88	387	1.01	433	
North Carolina	34°40'	1.04	Control:										Marshall, 1970
			Short	410	380	790	1.1:1	370	.93	-	-	-	
			Medium	680	400	1080	1.7:1	610	.89	-	-	-	
			Tall	1450	600	2050	2.4:1	1300	.90	-	-	-	
			Average	550	390	940	1.4:1	495	.90	-	-	-	
			+ Wastes:										
			Short	730	300	1030	0.24:1	663	.91	-	-	-	
			Medium	870	250	1120	0.22:1	770	.89	-	-	-	
			Tall	1970	720	2690	0.27:1	1735	.88	-	-	-	
North Carolina	34°40'	1.04	Tall	1550	650	2200	2.4:1	1300	.84	-	-	-	Williams & Murdoch, 1969
			Medium	750	750	1500	1.0:1	700	.93	-	-	-	
			Short	400	700	300	0.6:1	350	.86	-	-	-	
			Marsh average	545	424	808	1.3:1	474	.87	-	-	640	
Virginia	?	-	Tall	-	-	1570	-	-	-	-	-	-	Wass & Wright, 1969
			Medium	-	-	695	-	-	-	-	-	-	
			Numerical ave.	-	-	1140	-	-	-	-	-	-	
Virginia	37°41'	1.0	Marsh average	363	94	459	3.8:1	-	-	-	-	-	Mendelsohn, 1973
Maryland-Virginia	38°10'	.98	Short	558	150	608	3.7:1	-	-	-	-	-	Keefe & Boynton, 1973
			Short-mixed	518	256	774	2.0:1	-	-	-	-	-	
			Short-tall	427	280	707	1.5:1	-	-	-	-	-	
			Marsh average	506			2.1:1	-	-	-	-	-	
Maryland	38°35'	.49	Marsh average:										Cahoon, 1975
			1973	468	-	-	-	-	-	449	.97	-	
			1974	475	-	-	-	-	-	466	.98	-	
			Average	471	-	-	-	468	100%	457	.97	-	
Delaware	38°40'	1.4	Control-dwarf	-	-	-	-	-	-	-	-	1544 (fresh wgt)	Sullivan & Daiber, 1974
			N-added	-	-	-	-	-	-	-	-	1808 "	
			P-added	-	-	-	-	-	-	-	-	4208 "	
Delaware	38°50'	1.4	Mixed species	413	187	600	2.2:1	-	-	445	1.07	-	Morgan, 1961
			Monotypic	385	187	572	2.1:1	-	-	426	1.13	-	
New Jersey	39°10'	2.07	Marsh average (July 5)	-	-	300	-	-	-	-	-	-	Good, 1965

TABLE 1—Continued

Location	Latitude	Tidal Amplitude (m)	Marsh Type	Live (EOSL)	Dead (EOSD)	Total (EOST)	Ratio Live:Dead	Max-Min Method	% EOSL	Smalley's Method	% EOSL	Other	Source
New Jersey	39°40'	.73	Tall	1592	110	1702	14.5:1	-	-	-	-	-	Squiers & Good, 1974
			Short	592	90	682	6.6:1	-	-	-	-	-	
New York	40°40'	1.10	Short	-	-	508	-	-	-	-	-	-	Udell et al., 1969
			Tall	-	-	827	-	-	-	-	-	-	
			Marsh average	-	-	551	-	-	-	-	-	-	
Connecticut	41°00'	2.26	Tall										
			Greenwich 1	-	-	1325	-	-	-	-	-	-	Steever, 1972
	41°00'	2.26	Greenwich 2	-	-	1500	-	-	-	-	-	-	
	41°00'	1.80	Branford	-	-	1125	-	-	-	-	-	-	
	41°00'	1.64	Guilford	-	-	1050	-	-	-	-	-	-	
	41°10'	2.13	Westport 1	-	-	910	-	-	-	-	-	-	
	41°10'	2.13	Westport 2	-	-	1150	-	-	-	-	-	-	
	41°10'	2.13	Westport 3	-	-	1350	-	-	-	-	-	-	
	41°20'	1.37	Clinton	-	-	900	-	-	-	-	-	-	
	41°20'	1.07	Connecticut R.	-	-	900	-	-	-	-	-	-	
	41°20'	.82	Black Point	-	-	640	-	-	-	-	-	-	
	41°30'	.73	Stonington	-	-	600	-	-	-	-	-	-	
	41°30'	.73	Tall	717	187	904	3.8:1	-	-	820	1.14	-	
			Short	314	211	525	1.5:1	-	-	350	1.08	-	
			Numerical ave.	516	199	715	2.6:1	-	-	585	1.13	-	
Connecticut			Tall:										
	41°00'	2.26	Greenwich	682	17	699	40:1	-	-	-	-	-	Turner, unpub.
	41°00'	2.50	Rowayton	790	20	810	39:1	-	-	-	-	-	
	41°20'	2.35	Bridgeport	735	-	-	-	-	-	-	-	-	
	41°20'	2.13	Old Saybrook	879	-	-	-	-	-	-	-	-	
Connecticut	41°30'	1.7	High	-	-	470	-						Gross, 1966
			Streamside	-	-	487	-						
Rhode Island	41°20'-50'	1.40	Providence R. (tall) (avg. 3)	-	-	946	-	-	-	-	-	-	Nixon & Oviatt, 1973a
		1.16	Narragansett B. (tall) (avg. 7)	-	-	887	-	-	-	-	-	-	
		.79	Block Island S. (tall) (avg. 2)	-	-	840	-	-	-	-	-	-	
Rhode Island	41°30'	.24	Tall	-	-	840	-	-	-	-	-	-	Nixon & Oviatt, 1973b
			Short	-	-	432	-	-	-	-	-	-	
			Marsh average	-	-	466	-	-	-	-	-	-	
Massachusetts	41°30'	1.22	1971	350	-	-	-	350	1.2	360	1.0	-	Valiela et al., 1975
			1972	300	-	-	-	300	1.0	440	1.5	-	
			1973	400	-	-	-	400	1.0	720	1.8	-	
			August	350	-	-	-	350	1.0	510	1.4	-	
			+ Sewage: low treatment (ave. 3yrs)	-	-	-	-	-	-	860	-	-	
			high treatment (ave. 3 yrs)	-	-	-	-	-	-	1320	-	-	
Maine		1.5	(July) Streamside	-	-	703							Wiering, 1975 (pers. comm.)
Canada	44°45'	-	-	-	-	558	-	-	-	-		710	Hatcher & Mann, 1975
	45°50'	1.3	-	-	-	-	-	-	-	-		750	Martin, 1974 (cited in Hatcher & Mann, 1975)

t=2 as 950 g and 750 g, respectively. This is an incremental error of +100 g which is measured as production for that interval. If at t=3, the actual amounts are 800 g each of live and dead material, then with a potential error of ±50 g in the estimate, there are nine possible combinations of measurements at t=3, each with the same actual production for the interval, t=2 to t=3:

		Live material	Dead material	Estimated production	
1. Estimated at t = 2		950	750	—	
2. Actual at t = 2		900	700	0	
3. Actual at t = 3		800	800	0	
4. Measured at t = 3: (±50 g error)	a)	800	800	—100	(disregarded)
	b)	800	750	—150	"
	c)	800	850	— 50	"
	d)	850	800	— 50	"
	e)	850	750	—100	"
	f)	850	850	0	"
	g)	750	800	—150	"
	h)	750	750	—200	"
	i)	750	850	—100	"

TABLE 2

Net above-ground production for other salt marsh macrophytes (g dry wt m^{-2} yr^{-1})

Location	EOSL	EOSD	EOST	Max-Min	Smalley	Other	Author
Spartina patens (SP)							
Connecticut	294	510	804	-	360	-	Steever, 1972
New York	-	-	991	-	-	-	Harper, 1918
New York	-	-	503	-	-		Udell *et al.*, 1969
New Jersey, 1969	343	381	724	-	-	-	Nadeau, 1972
New Jersey, 1970	463	160	623	-	-	-	
Virginia	-	-	805	-	-		Wass & Wright, 1969
North Carolina, 1965	559	996	1555	406	1453	-	Waits, 1967
North Carolina, 1966	720	178	898	451	1140	-	
Louisiana	895	790	1685	-	2128	-	Payonk, 1975
Mississippi	1242	-	-	-	1922	-	de la Cruz, 1974
Distichlis spicata (DS)							
Connecticut	359	526	885	-	300		Steever, 1972
New York	-	-	647	-	-	-	Udell *et al.*, 1969
New Jersey	565	410	985	-	-		Morgan, 1961
Virginia	-	-	360				Wass & Wright, 1969
Georgia (Sept)	246	357	603	-	-		Gallagher *et al.*, 1972
Mississippi	1072	-	-	-	1484		de la Cruz, 1974
Juncus sp. (J)							
Connecticut	566	258	851	-	570		Steever, 1972
Virginia	-	-	650	-	-	-	Wass & Wright, 1969
North Carolina	1173	915	2088	654	796	478[1] 1215[2] 560[3]	Stroud & Cooper, 1968
North Carolina	1127	1500	2627	-	-	754	Williams & Murdoch, 1972
North Carolina	405	840	1245	-	-	560[4]	Foster, 1968
Georgia (Sept)	913	625	1538	-	-	-	Gallagher *et al.*, 1972
Georgia	1300	-	-	-	-	2261	Reimold *et al.*, 1975
Mississippi	-	-	2000	-	-	-	Eleuterius, 1972
Mississippi	1300	-	-	-	1697	-	de la Cruz, 1974
Florida (May)	232	617	849	-	-	-	Heald, 1969
Spartina cynosuroides (SC)							
Virginia	546	442	998	-	563	-	Mendelsohn, 1973
Virginia	-	-	1456	-	-	-	Wass & Wright, 1969
Georgia site I	785	125	910	-	-	-	Odum & Fanning, 1973
Georgia site II	762	110	872	-	-	-	
Georgia site III	515	310	825	-	-	-	
Georgia site IV	1242	850	2092	-	-	-	
Georgia site (whole area)			1028				
Mississippi	1862	-	-	-	2190	-	de la Cruz, 1974
Mixed sp. (dominants)							
Connecticut (DS/SP)	441	492	934	-	440	-	Steever, 1972
Maryland (streamside)	1246	-	-	-	-	-	Johnson, 1970
Maryland (mixed)	1207	-	-	-	-	-	
Maryland (SA/DS)	518	396	914	-	-	-	Keefe & Boynton, 1973
Maryland (SP/DS)	634	-	-	606	617	-	Cahoon, 1975
Maryland (SP/other)	675	-	-	672	-		
Virginia (SA/SP/DS)	467	333	800	-	572		Mendelsohn, 1973
North Carolina							
(SP/DS) 1965	792	815	1607	573	1478		Waits, 1967
(SP/DS) 1966	939	1310	2249	500	1190		
(SP/DS/J) 1966	600	944	1544	-	621		
Mississippi (mixed)	1592	250	1842	1051	-	1108	Gabriel & de la Cruz, 1974

[1]Computer model including turnover of live leaves.
[2]Computer model including turnover of live and dead leaves.
[3]Computer model developed by Williams and Murdoch (1972).
[4]Average of 2 methods incorporating rates of growth and decay of leaves.

Thus the +100 g error from the previous interval is not corrected. If the standing biomasses of live and dead material are measured as 850 and 650 g at t=2, the −100 g error in the estimate of production from t=1 to t=2 is disregarded in accumulating the annual production for all intervals. However, the error within the estimate is carried forward to estimate the production between t=2 and t=3. In this case there are several possible results (using the same possible ± g error in estimating the amounts) which range from 0 to 200 g production. Thus the −100 g error from the previous interval (t_1 to t_2) *may be* corrected.

In the expanding matrix of the possible situations when live material is decreasing between intervals, only positive errors in the estimations of the actual amounts present tend to accumulate without correction, and there is a statistical problem that one is left with in order to estimate the magnitude of the cumulative error. Since the sampling covariance may be up to 0.50 (e.g., in Smalley 1958) the example of a ±50 g error is realistic.

The other methods have inadequacies for which Smalley's method attempts to compensate. They do not account for the turnover of live and dead material during the year. Besides unmeasured herbivory between sampling periods, both tides and a favorable growing season may influence this turnover rate.

Keefe and Boynton (1973) have suggested that tides influence the turnover of dead material on the marsh. This is borne out by the data. The ratio of live: dead material on a marsh increases with increasing tidal amplitude (Fig. 3). Turnover of live and dead material between sampling dates is what Smalley's method seeks to estimate. However, as Smalley (1958) acknowledges, even if statistical errors are presumed nil, the method still underestimates production at times. For example, if 50 g turnover each of live and dead material occurs during the sampling interval and 50 g of growth occurs as well, the latter is not measured. For the sampling interval, the measured difference in live biomass will be zero (50 g growth—50 g death) as will the measured difference in dead biomass (50 g death—50 g lost); thus the 50 g of production is not measured.

There are examples of this rapid turnover of dead material in several seasonal studies. For example, Smalley (1958) measured decreases in live material for 2 months in the fall on a streamside levee site. For the same period there was no dead material present in spite of 233 g m^{-2} formation of dead material in the intervening period. Young's (1974) data for a Florida salt marsh suggest that higher temperatures may also stimulate turnover of dead and live material. In Florida and Texas marshes the weight of dead culms is 25–50% less than live

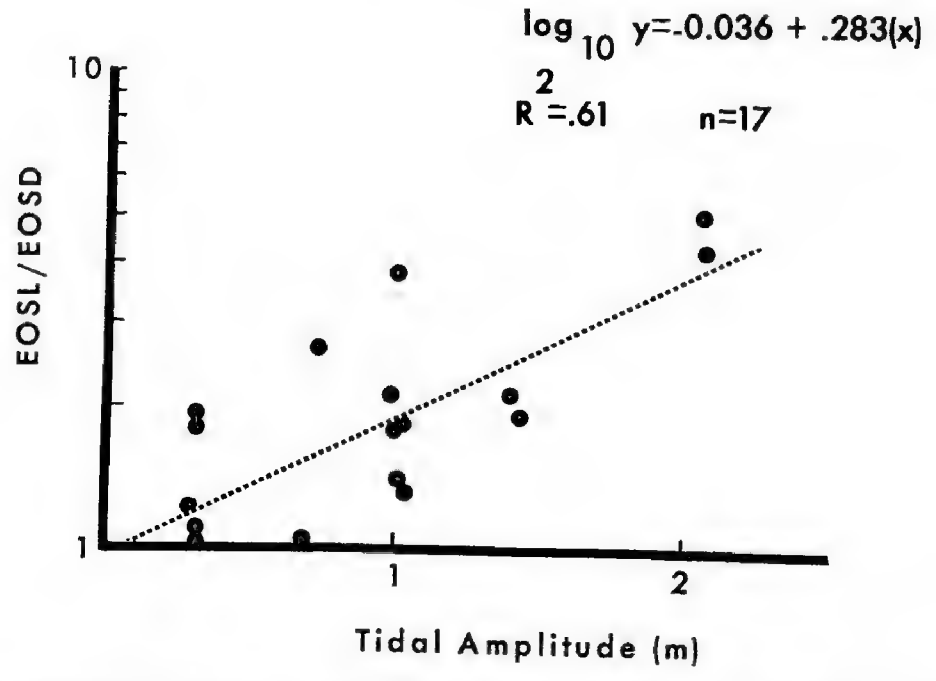

FIG. 3. The relationship between end-of-the-season live/dead material (EOSL/EOSD) and mean tidal amplitude in the marsh.

culms (Turner and Gosselink 1975). In addition, usual practice does not include estimates of leaf losses simultaneously with Smalley's method. These leaf losses average 21% of the EOSL estimates (Table 3). The estimates may not be strictly comparable since Hatcher and Mann's (1975) estimate included leaves still attached to the plant while Williams and Murdoch (1969) and Odum and Fanning (1973) included only leaves lost as evidenced by leaf scars on the culm.

The arrangement of the data in Figure 3 also suggests that high energy environments move material off the marsh faster than low energy environments. Though an obvious conclusion, perhaps, a higher energy environment implies a shorter residence of particulate material on the marsh, which means less time available for surface colonization of the plant by epiphytic producers and consumers, including nitrogen fixers which can be significant components of the system (Stowe 1972, Ruinen 1971). Their presence or absence may also influence the quantity and quality of organic matter available to the estuarine ecosystem.

Kirby (1972) and Reimold *et al.* (1975) were the only published references found, while conducting this review, where a variation of Wiegert and Evans's (1964) approach was used to estimate turnover for a *S. alterniflora* marsh. However, work is in progress in Louisiana and elsewhere which employs the paired-plot method (Gosselink, personal communication). The net annual production was estimated to be twice the year-end standing biomass (live) and was considerably higher than the estimates obtained using Smalley's method (e.g. 1647 vs. 1138 g dry wt m^{-2} yr^{-1}). For *Juncus roemerianus*, Williams and Murdoch (1972) have demonstrated the importance of including turnover measurements for both live and dead material. Furthermore, relative to EOSL estimates, turnover appears to be greater in warmer climates (Table 4). Dead material is not completely cleaned off the marshes during the winter—even in Connecticut (Steever 1972). Given the various factors known to influence the turnover of

TABLE 3

Estimates of annual organic material lost in the form of leaves as a percentage of the end-of-the-year standing biomass of live material (EOSL) for *Spartina alterniflora*

Marsh location	Percent leaf loss	Author
Canada		
Tall	23.3	Hatcher & Mann, 1975
Medium	27.1	
Short	35.1	
Average	28.5	
North Carlina		
Marsh average	19.3	Williams & Murdock, 1972
Georgia		
Streamside	22.4	Odum & Fannings, 1973
Medium and low marsh	8.9	
Average	15.6	
Mean for 3 locations	21.1	

TABLE 4

The relationship between 1) production estimated by end-of-year harvest (EOSL) and 2) seasonal changes in live and dead material (Smalley's method) at different locations in the U.S. for various macrophytes

	Spartina alterniflora		Spartina patens		Distichlis spicata & S. patens		Spartina cynosuroides		Juncus sp.	
Location	range	mean	range	mean	range	mean	range	mean	range	mean
New England	1.00–1.80	1.25	1.00	1.00	1.00–1.02	1.01	–	–	1.00	1.00
Chesapeake Bay	1.00–1.10	1.05	–	–	1.22	1.22	1.13	1.13	–	–
North Carolina	.98–1.27	1.01 1.10[1]	1.58–2.60	2.09	1.27–1.87	1.57	–	–	1.20–1.38	1.29[2]
Georgia	.89–1.36	1.15	–	–	–	–	–	–	–	–
Louisiana	1.20–1.38	1.35	–	2.37	–	–	–	–	–	–
Mississippi[3]	1.30	1.30	1.55	1.55	–	–	1.18	1.18	1.30	1.30

[1]Based on a computer "curve-fitting" model.
[2]Based on a computer model calculating turnover of live and dead leaves (from Williams & Murdoch 1972).
[3]Based on May-August sampling only (fall form).

dead material, a good measure of variability is added to comparisons of annual production using EOST estimates.

This discussion has not included below-ground production. There are as yet only four measurements of below-ground biomass. Root biomass is equal to shoot biomass in Massachusetts (Valiela and Teal 1974), is "several times higher" and three times higher in North Carolina (Williams 1972; Cammen *et al.* 1974, respectively) and 10 times greater in Louisiana (Patrick and Delaune, personal communication). Mutah *et al.* (1968) have shown that for a wetland community, *Miscanthus sacchariflorus*, the seasonal variation in below-ground root and rhizome biomass may be 50%, the production exceeding that of the variation in above-ground biomass. The importance of this to the above-ground consumers has barely been investigated. Does this root mass "leak organics" in significant amounts? Is it important to benthic regeneration of nutrients or benthic consumer organisms?

Variations with Latitude

There is a definite latitudinal gradient in annual marsh production, regardless of which method is used to estimate it (Fig. 4; Tables 1, 2, 4). Estimates using Smaller's method demonstrate this clearly. There is also a latitudinal gradient of live biomass which over-winters (Fig. 5).

Seasonal growth of *S. alterniflora* begins in the spring and ends in the fall in fall in northern North Carolina (Williams and Murdoch 1969). Farther south, Stroud and Cooper (1968) observed some young shoots present throughout the year. Kirby and Gosselink (1976) have suggested that in the Gulf, with a longer growing season and mild winters, understory development may progress con-

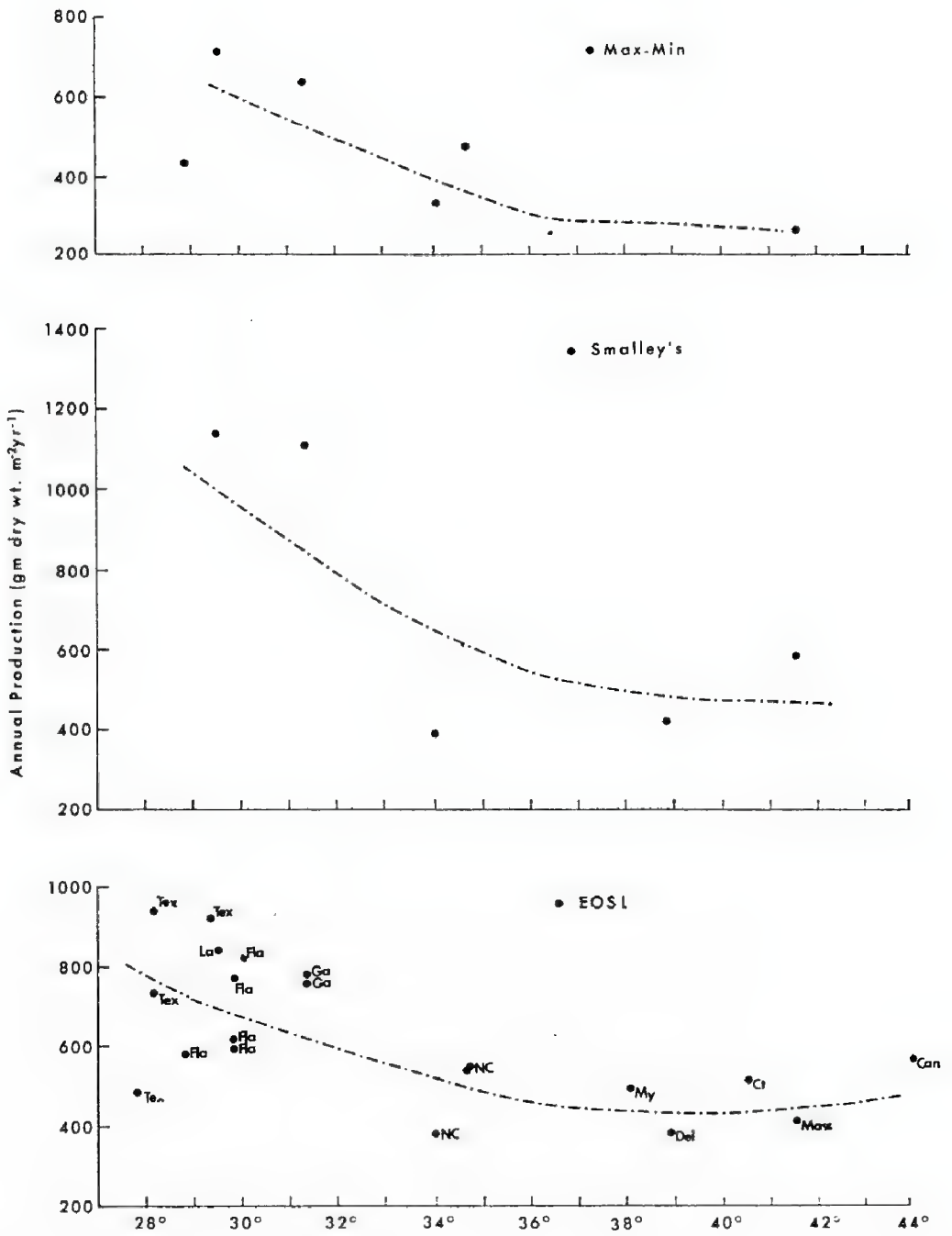

FIG. 4. The relationship between latitude and annual production estimates of *S. alterniflora*. Top: Max-min method; Middle: Smalley's method; bottom: EOSL estimates. Curves fit by eye.

tinuously most of the year. Thus if the turnover rate is positively dependent on the disappearance of material per g standing crop of live material and does not vary with latitude, the more southerly marshes will have a higher production because of a higher mean annual standing crop.

The north-south gradient in marsh production should be expected in view of our knowledge of other species. Geographic variations in the annual growth of plants with similar physiology, forest litterfall, and net ecosystem production are closely correlated to those factors which measurements of latitude integrate, especially temperature and sunlight (Fogg 1973, Spence 1964, Bray and Gorham 1964, and Rosenzweig 1968). Also, the seasonal growth of *S. alterniflora* is very closely related to temperature, and the net growth changes in a consistent manner with changes in latitude (Turner 1975b).

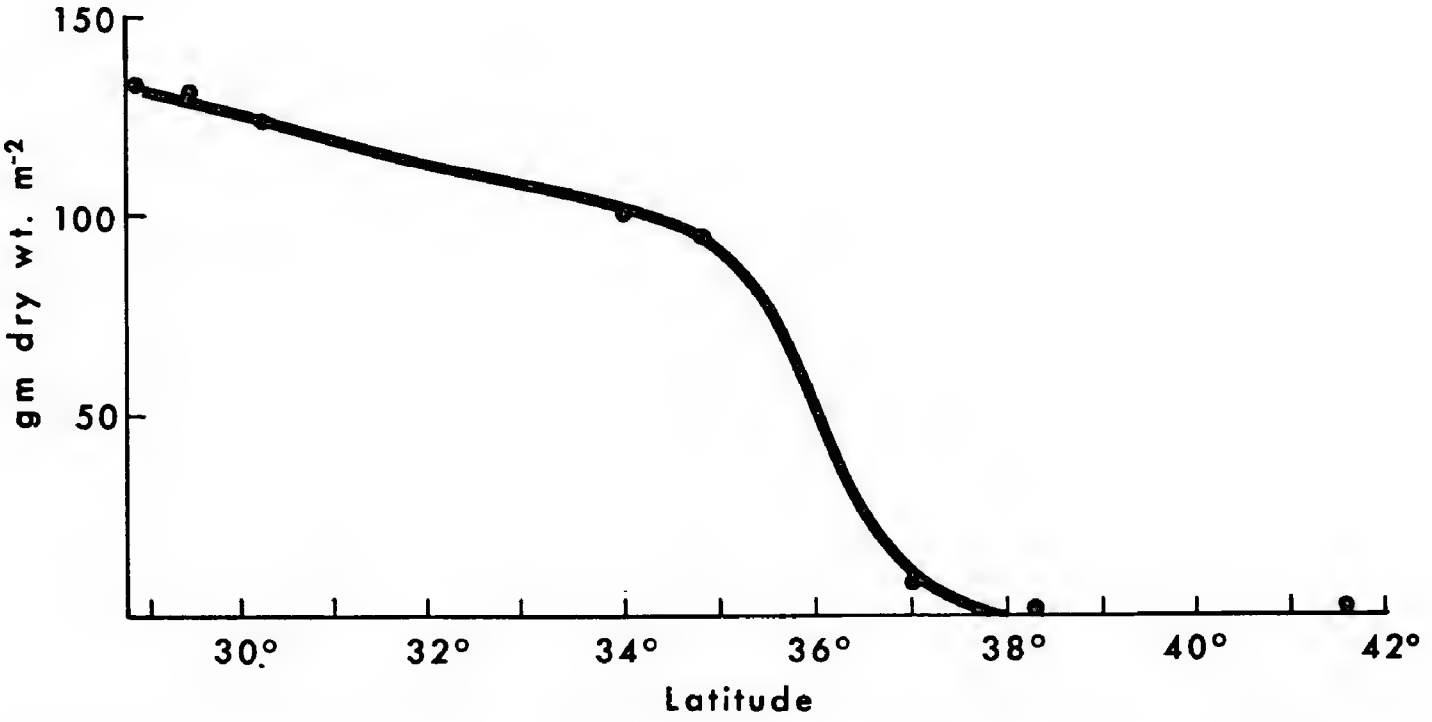

FIG. 5. The relationship between latitude and the winter (minimum) amount of biomass found on the marsh. Curve fit by eye.

Regional Variability

There is, however, a great deal of variability in the estimates among different locations at any one region. Two whole-marsh averages taken during different years in Georgia are similar, even though different techniques were used to measure EOSL. Sampling repeated during successive years in Massachusetts, Maryland, North Carolina, and Georgia (Valiela and Teal 1974, Valiela *et al.* 1975, Cahoon 1975, Williams and Murdoch 1969, Smalley 1958) resulted in similar EOSL values within each marsh. Thus, the production estimation differences within and between regions are probably real. In fact, the variation in EOSL values for *all S. alterniflora* marshes is similar to the variation within any one region (Table 5) and the mean latitudinal difference between marshes is less than the difference between streamside and high locations within most marshes.

TABLE 5

Variations in average marsh production within one region (above-ground EOSL values from Table 1)

Location	n	Mean	Standard deviation	Coefficient variation
Texas	4	756	237	.31
N. Florida	4	701	114	.16
Louisiana	5	643	186	.29
Georgia	1	762	—	—
N. Carolina	3	497	86	.17
Chesapeake Bay area	4	431	68	.16
New England	2	418	139	.33
All sites	23	620	177	.29

Previous investigations have suggested several factors other than latitude which might influence annual production and thus variability. These are tidal amplitude, nutrient availability, and salinity.

The relationship between streamside and marsh average production is very weak (Fig. 6). There was no statistically significant relationship for all sites between marsh average production (or streamside production) and tidal amplitude (Fig. 7). However, there was a very good statistically significant relationship between tidal amplitude and EOST at *streamside* sites in Long Island Sound (Warren *et al.* 1976) (coefficient of determination, $R^2 > .90$). There is not yet a clear explanation for this relationship. Nixon and Oviatt (1973a) point out that nutrient concentrations in waters flooding the marshes in Narragansett Bay are high where biomass is high. Sediment nitrogen and phosphate and surface ammonia concentrations were statistically significant variables in their multiple regression analysis of the local variation in streamside EOST. Tidal amplitude (Tide Tables, 1973) is greatest in the upper part of the bay where production was the greatest. At site H (in the bay), the mean tidal amplitude, however, was a very low 0.24 m (Nixon and Oviatt 1973b). There the biomass was equal to the mean EOST for all 12 sample sites in the area (range 433–1380 g dry wt m^{-2}) similar to that at nearby Stonington, Connecticut (Steever 1972) and also to that at the Great Sippewissett marsh in Massachusetts (Valiela and Teal 1974), despite tidal amplitude ranges in these areas of 0.24 m, 0.73 m, and 1.22 m,

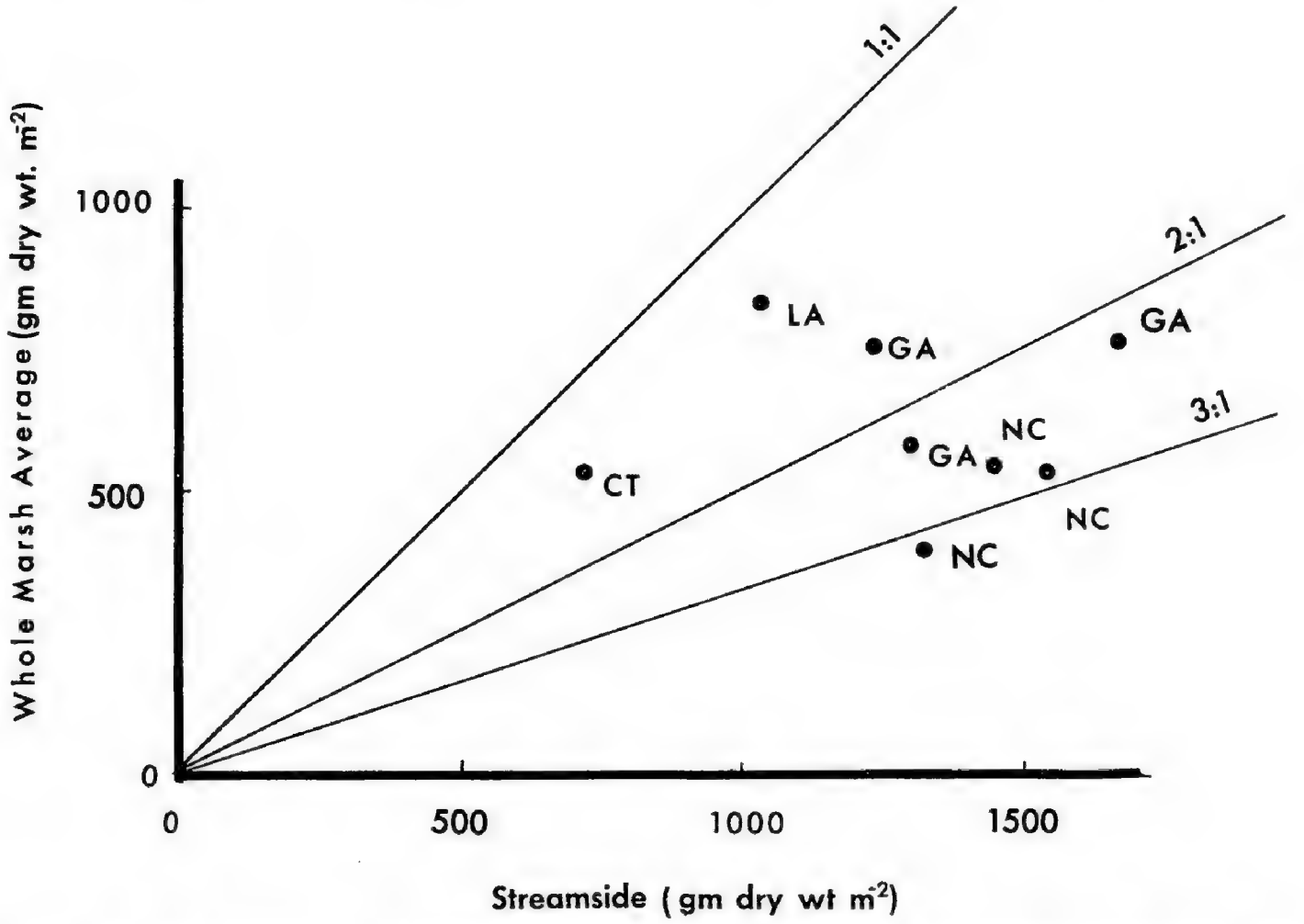

FIG. 6. The relationship between average marsh biomass and streamside biomass in late summer (EOSL values).

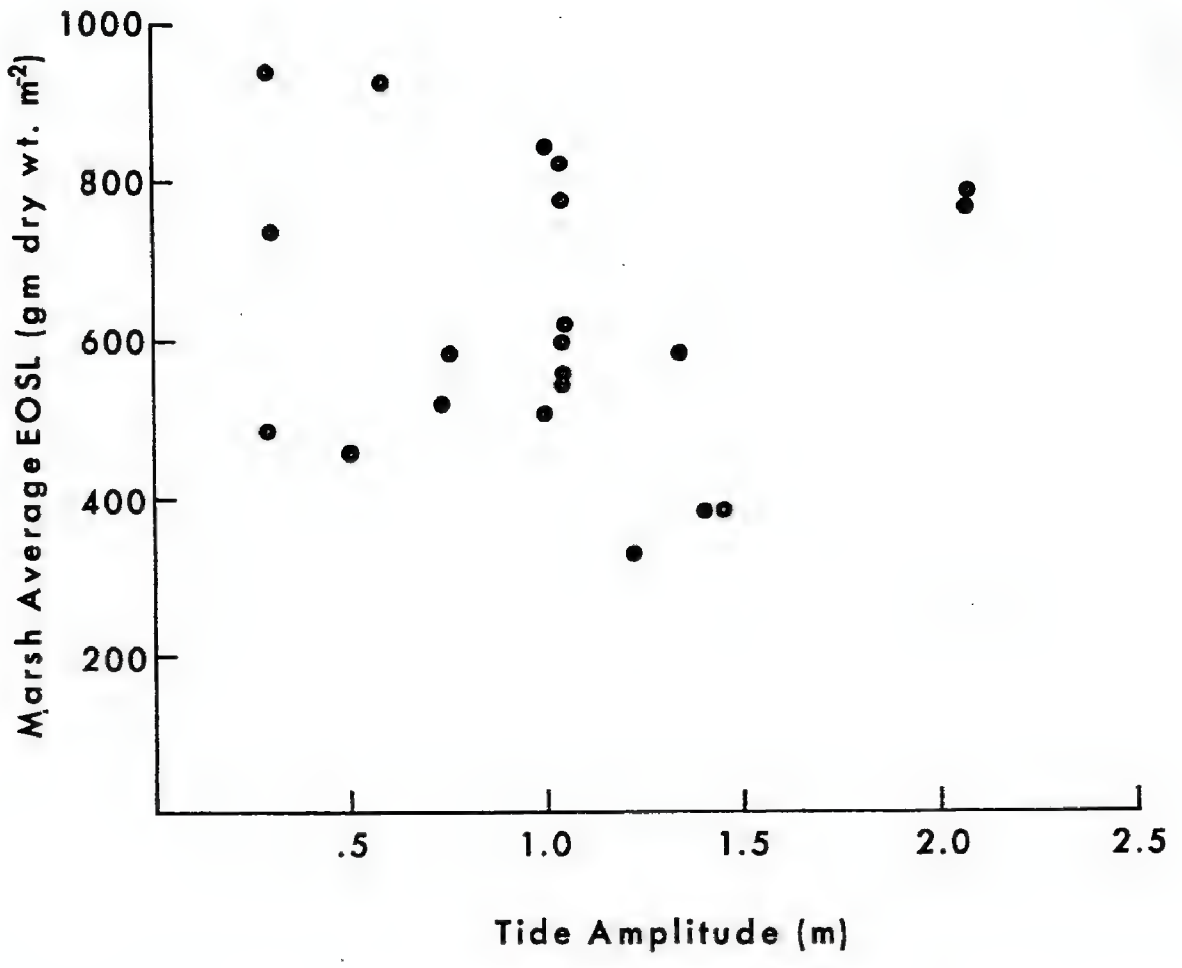

FIG. 7. The relationship between tidal amplitude and end-of-the-season biomass of live material (EOSL) for the entire marsh.

respectively. When nutrients, particularly nitrogen, are applied topically to salt marshes, an increase in production is usually observed (Valiela and Teal 1974, Tyler 1967, Marshall 1970, Sullivan and Daiber 1974, Payonk 1975). Long Island Sound surface waters had a nutrient concentration gradient from east to west in 1952 (Riley 1959, Riley and Conover 1956) which coincides with the observed gradient in streamside biomass. In 1971, however, this was not observed (Warren *et al.* 1976). For the Florida and Texas marshes, tidal amplitudes are nearly equal (but low) yet the variation within the regions is considerable. It seems possible, therefore, that variations in tidal amplitude per se are not the primary factor regulating latitudinal variations in *total* marsh productivity, but that they may strongly influence local streamside productivity. This is not meant to suggest that tides do not influence the geomorphology, plant species distribution, or other aspects of the marsh structure and function.

Surface water salinity did not appear to be a significant variable in a step-wise regression analysis of variability of production in Rhode Island marshes (Nixon and Oviatt 1973a). Investigating variations in soil water salinity may be a more fruitful approach. Laboratory results have shown a response of *S. alterniflora* growth to changing salinity (Adams 1963, Phleger 1971). As Nixon and Oviatt (1973a) point out, however, the wide local salinity fluctuations which occur in most marshes and the matrix of variables involved seem to prohibit a simple application of these laboratory results to a complex field situation.

Solar Conversion Efficiency

The maximum annual macrophyte production for the salt marshes reported here is 2 to 4 times the minimum, depending on the method of measurement. This is a rather small variation and similar to differences in other environmental parameters (Table 6). An interesting relationship is that between annual solar radiation (measured at the surface, Budyko 1974) and annual production. There is a considerable variation between marshes but the trend is clearly one of similar conversion efficiency at all locations if end of the season biomass estimates are used (Fig. 8). If an upper estimate of annual production is used (assuming 21% leaf losses, a turnover, relative to EOSL, of 40% in southern latitudes and 10% in northern locations), there is then a parallel but higher efficiency. The conversion efficiency of 0.20–0.35% would be even higher if below-ground production were included. To put these estimates into perspective, the total marsh system production may be higher by the following amounts:

Production	g m^{-2} yr^{-1}	Source
Above-ground	300–800	Tables 1, 2
Epiphytic (La.)	60	Stowe 1972
Leachate	100–350	Turner 1975a
Benthic	40–230	Gallagher 1971, Pomeroy 1959, Brkich 1972 (in Day *et al.* 1972)
Below-ground	?	

An intramarsh difference in the efficiency of converting solar energy into plant matter is apparent for streamside and high marsh locations (Fig. 9). Only stream-

TABLE 6

A comparison of selected environmental factors at several coastal locations

Location	Annual Hours of Sunshine[1]	Avg. Annual Temp. C[1]	Heating Degree days (18.3 C base)[1]	Evapotranspiration[2]	Avg. Solar Input (g cal/cm^{-2} day^{-1})[3] Annual	August
Portland, Maine	2261	7.2	4172	549	350	488
Boston, Mass.	2247	10.8	3129	642	301	411
Cape Hatteras, North Carolina	2349	16.8	1451	860	443	562
New Orleans, Louisiana	2813	20.3	769	1099	347	416
Tampa, Florida	2963	22.3	379	1215	453	494

[1] U.S. National Weather Summary, 1972.

[2] Computed using equations of Thornthwaite and Mather (1957).

[3] From National Atlas of the United States, 1966. U.S. Dept. Commerce, averages are for a 9-11 yr period.

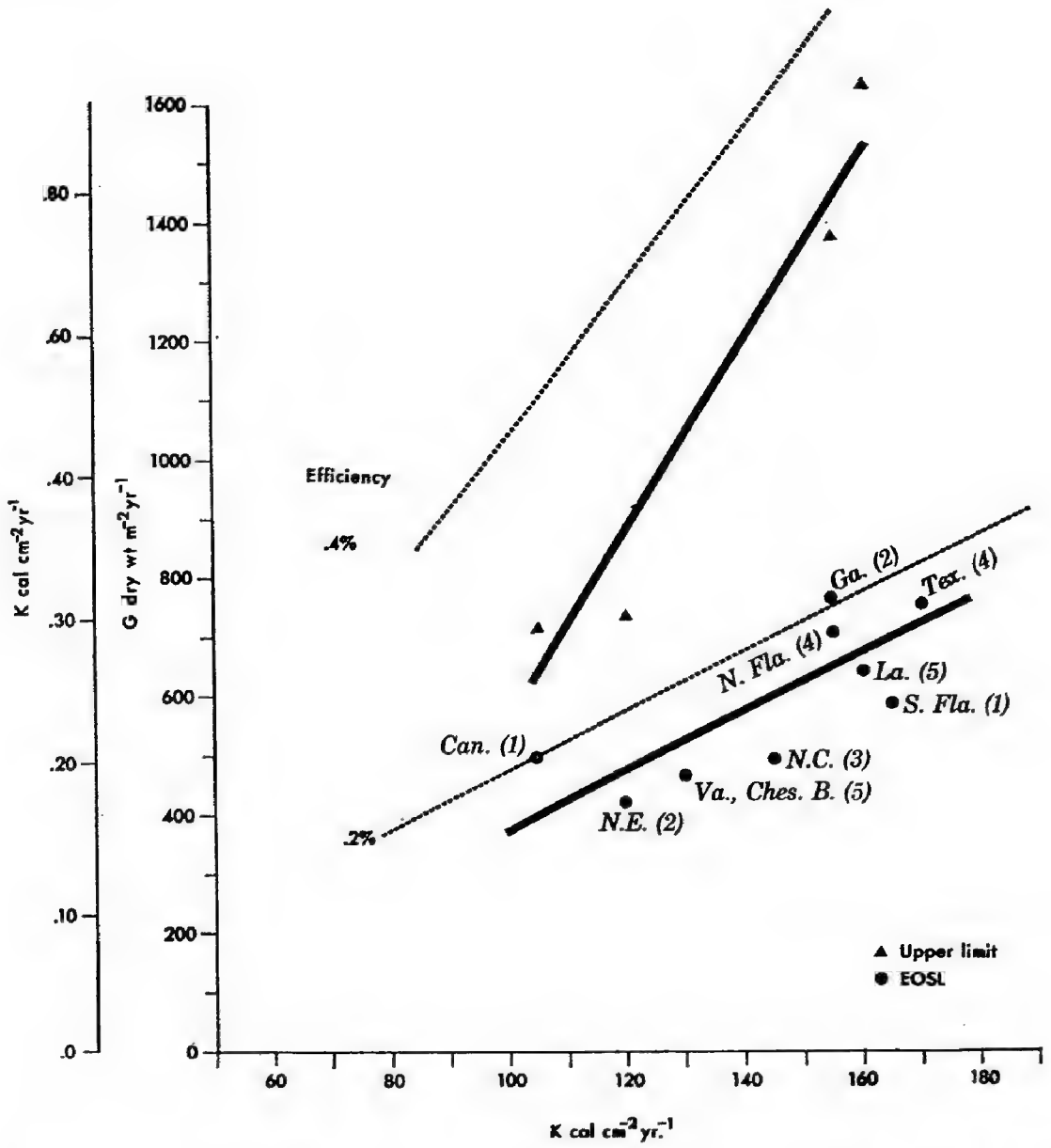

FIG. 8. Average *S. alterniflora* annual marsh production as related to solar energy inputs (measured at the earth's surface, from Budyko 1974). Averages are for 10 regions using end-of-season live standing biomass (EOSL) estimates from Tables 1 and 5, and upper estimates for the northern and southern locations. Dotted lines represent a solar conversion efficiency of 0.2 and 0.4%.

side marshes are left at the southern limit of *S. alterniflora*, which may indicate something about its nutrient cycling system. If factors controlling net production within marshes were similar then a parallel line would be expected for both locations. They are not parallel and the Gulf coast streamside marshes are conspicuously different from the others.

Comments

Some of these estimates may represent a biased sampling. It seems likely that ecologists attempting to comprehend ecosystem functions would select a "healthy" or "natural" marsh rather than a "stressed" marsh to study. The selection of marshes to study which are less productive than nearby ones has probably been avoided more often than not. Yet, these marshes which are 1) abnormal, 2) stressed, or 3) other members of the data set (depending on one's viewpoint),

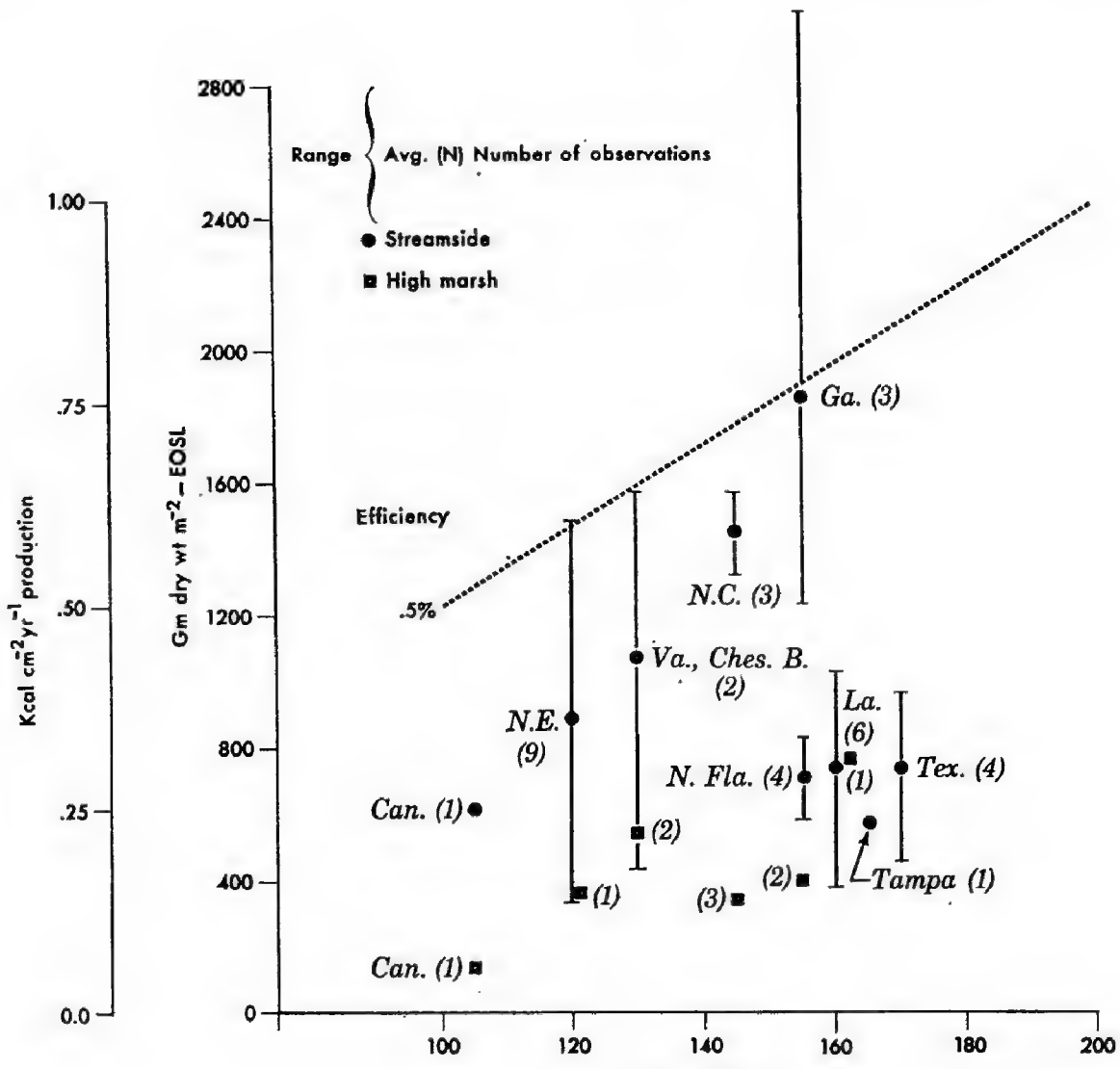

FIG. 9. *S. alterniflora* annual production at streamside and high marsh locations as a function of solar energy inputs (measured at the earth's surface, from Budyko 1974).

may represent very suitable sites for a study of factors which influence marsh variability such as tidal circulation, geochemical interactions, sediment consolidation, or recent depositional activities.

Although a great deal of attention has been given to *S. alterniflora* marshes, the area dominated (in floristic composition) by other plants is considerable (Table 7). Tables 1 and 2 cite 29 references for *S. alterniflora* yet only 23 for all other species (4 differsent monotypic associations and mixed species). Although more is known now than in the past about salt marshes, it is necessary to be selective in what data are collected, but the data available are indicative of the previous levels of research support. Salt marshes have often been described as nursery grounds for the coastal water fisheries in the Gulf of Mexico. Without making a qualitative judgement, it should be noted that relative to other areas in the United States there has been less research there than on the Atlantic coast, although comprising 60% of the U.S.'s coastal marshes (Turner and Gosselink 1975). For example, only 10 of a total of 44 references in Tables 1 and 2 concern themselves with this area. Hopefully this will change considerably as more emphasis is placed on the value of renewable resources and a greater appreciation

TABLE 7

Distribution of salt marsh species by area at selected locations

Location	Total Marsh Surface[1] (10^3 ha)	Dominant Plant: % Spartina Alterniflora (SA)	% Spartina patens (SP)	% Distichlis spicata (DS)	% Juncus sp. (J)	% Mixed Community & Other	Author
Atlantic Coastal States, 1954	718.4	52	25		23	-	Spinner, 1969
Rhode Island	.017	78	19		-	3	Nixon & Oviatt, 1973b
Connecticut	.012	45	-	-		55 (SP,DS,J)	Steever, 1972
Maryland	.026	36	60	-	1	3	Nadeau, 1972
North Carolina	.767	88	-	-	12	-	Stroud & Cooper, 1968
North Carolina	83.3	28				62 (all others)	Wilson, 1962
Georgia (Duplin River)	1.1	94	-	-	6		Gallagher et al., 1972
Mississippi	25.9	3	<.1	-	96		Eleuterius, 1972
Louisiana							
Saline zone	199.8	62	6	14	10	8	Chabreck, 1972
Brackish zone	327.1	5	55	13	4	23	
Intermediate	153.4	< 1	34	0	1	66	
Fresh water zone	315.5	0	4	0	1	95	

[1] Exclusive of water area.

is more widely felt for the necessity to develop a thorough comprehension of the important biological processes.

SUMMARY

Of the several methods used to estimate net above ground production, Smalley's (1958) has been widely employed. There is a problem determining how accurate the method is, and it does not measure the significant amount of leaf losses which occurs (Table 3). Nevertheless, it is a more preferable method than annual estimates based on end-of-the-season live and total biomass. The measured turnover of dead and live material would prove to be higher and more accurately reflect true net production if other methods were used (e.g., Wiegert and Evans 1964, Lominicki *et al.* 1968, Williams and Murdoch 1972). Apparent turnover of dead material is dependent on physical forces such as tidal amplitude (Fig. 3) and, in general, seems to increase with temperature (Table 4). Estimates of annual production by salt marsh macrophytes range from 300–2000 g dry wt m^{-2} yr^{-1} (Tables 1 and 2) and increase with a decrease in latitude. The solar conversion efficiency is from 0.20 to 0.35% and could possibly be up to 3 times higher if below-ground, epiphytic, and benthic production and leachate losses were included. Variation between and within marshes is apparent and is influenced by physical factors in ways not yet completely understood. Current research emphasis has centered around nutrient availability but geological and physical factors need to be considered more thoroughly.

ACKNOWLEDGMENTS

This manuscript has benefited from comments by J. G. Gosselink, S. W. Nixon, L. R. Pomeroy, D. S. Ranwell, S. W. Warren, and one unidentified reviewer as well as colleagues in the Systems Ecology program at LSU. I would also like to thank W. A. Niering, A. A. de la Cruz, W. H. Patrick, Jr., and D. L. Young for the use of unpublished data. This work is a result of research sponsored by the Louisiana Sea Grant Program, which is part of the National Sea Grant Program maintained by the National Oceanic and Atmospheric Administration of the Department of Commerce.

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STRESS AND COMMUNITY STRUCTURE OF MACROBENTHOS IN A GULF COAST RIVERINE ESTUARY[1]

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ABSTRACT

Effects of salt water intrusion and industrial effluents on community structure of benthic macroinvertebrates of the Neches River estuary were studied from 1967 to 1972.

Estuarine species comprised 50% or more of the total taxa at downriver stations. Maximum numbers of taxa and densities occurred within the salt water wedge. At upriver stations estuarine species were common during periods of salt water intrusion. Maximum numbers of taxa and densities occurred during freshwater conditions.

Diversity (d) generally decreased downriver and ranged from below 1.0 in the industrialized reaches to above 3.0 at upriver stations when salt water was not present. Diversity values lower than 2.5 occurred several times due to redundancy of "clean water" species.

INTRODUCTION

Benthic macroinvertebrate communities are very sensitive to environmental stress. Thus, they are often used by water quality biologists to detect effects of environmental perturbations. The Environmental Protection Agency (1973) encourages their biologists to used the Shannon-Weaver diversity index applied to benthic communities as an indication of water quality.

Many investigators have determined the effect of various types of stress on diversity of benthic communities. However, few studies have been published on diversity fluctuations of estuarine benthic communities. Wilhm and Dorris (1968), using data from Reish and Winter (1954), determined the effects of storm sewer effluent on diversity of benthic communities in Alamitos Bay. Boesch (1972) reported on diversity of benthic communities in marine and estuarine soft mud habitats. Holland *et al.* (1973) used diversity of benthic macroinvertebrates as an indication of water quality in Galveston Bay. This report is con-

[1] Supported by Office of Water Resources Research Grant B–106–Texas and Lamar University faculty research funds.

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cerned with effects of salt water intrusion and industrial wastes on community structure of benthic macroinvertebrates in the Neches River estuary, Texas.

AREA, STATIONS AND METHODS

Description of Area

The Neches River flows southeasterly over an axial distance of 338 km (210 mi), and empties into Sabine Lake, an inlet of the Gulf of Mexico (Texas Water Development Board 1966). The river is vital to the economy of the area for navigation and as a water supply. The lower 33.8 km (21 mi) of the river have been dredged to a depth of 12 m (40 ft) forming the Neches Ship Channel. The water of the river is used to supply: (1) a large industrial complex consisting primarily of petrochemical refining and manufacturing, and production of lumber products, (2) municipal water for over 350,000 people, and (3) irrigation for as much as 24,281 ha (60,000 acres) of rice land.

Much of the water is distributed by the Lower Neches Valley Authority (LNVA). The water is pumped from two stations located on Pine Island Bayou tributary (Fig. 1). The water demand of the LNVA ranges from 20 to 50 m^3/sec (800 to 2000 cfs), depending on the season. Much of this water is returned to the river below km 33.8. However, by this time many types of pollutional effluents have been added.

When river discharge is 28 to 42 m^3/sec (1000 to 1500 cfs) above the demand of the LNVA the waste effluents are carried downriver, and eventually into the Gulf of Mexico. When river discharge is less than this the LNVA installs temporary salt water barrier dams across the river at km 59 (mi 37) and across Pine Island Bayou at km 4.8 (mi 3) to protect their freshwater intakes from salt water intrusion (Fig. 1). These barrier dams divert the entire flow of the river

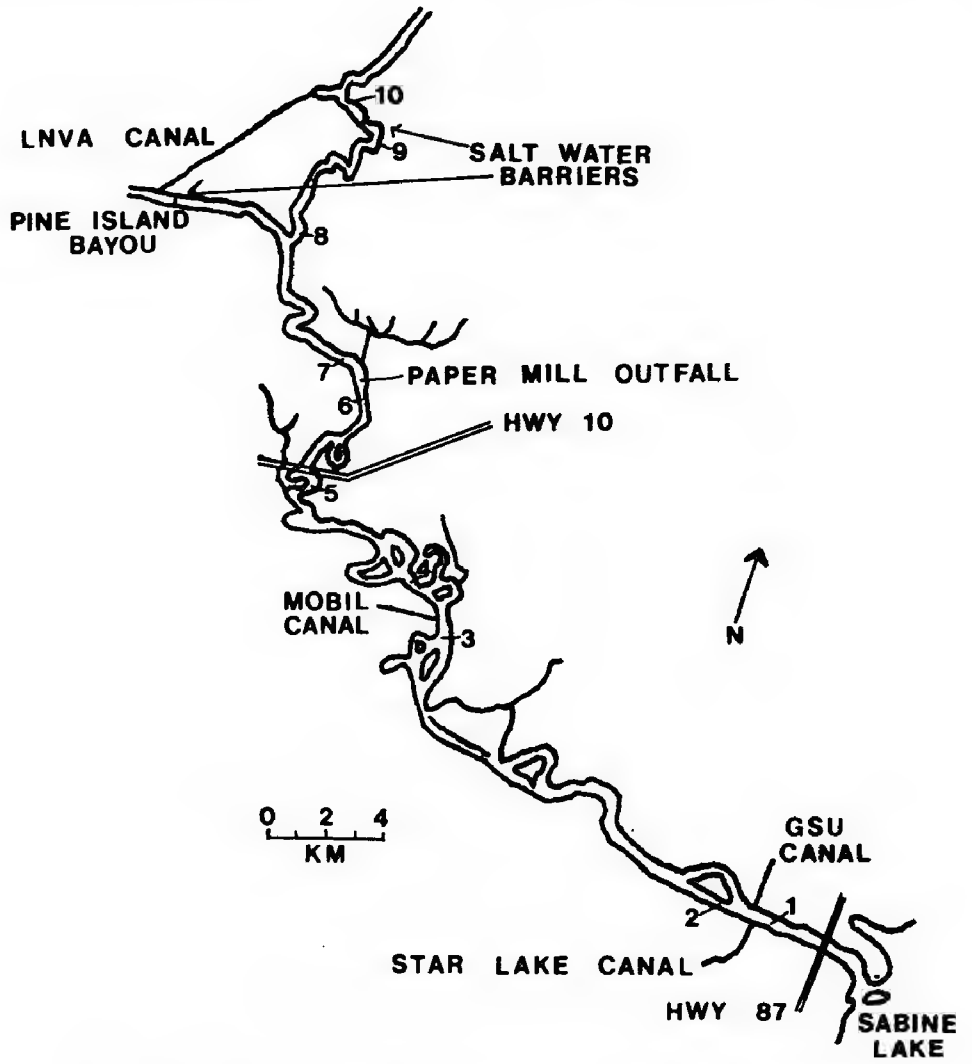

FIG. 1. Location of Neches River sampling stations.

into the LNVA Lakeview Canal, and allow salt water from the Gulf and pollutional effluents from the lower river to move up to the salt water barrier dams. Tidal action flushes the salt-waste water back and forth causing it to become more concentrated the longer the barriers are in place.

The temporary barrier dams have been installed every year since 1951, except 1968 when an unusually large amount of precipitation occurred during the period of high water demand. In 1969 only the Pine Island Bayou barrier was installed.

Stations

Benthic macroinvertebrates and selected physicochemical data were collected approximately 40 meters above and below the Neches River barrier in September, 1967 after two months of salt water intrusion. In June, 1970 samples were collected at the Neches River barrier site before installation, at selected time intervals 40 meters above and 40 meters below the barrier while it was in place, and after removal in August until December, 1970. During August, 1970 samples were collected above and below the Pine Island Bayou barrier. In 1971 the salt water barrier dams were installed in June, and sampling was resumed in September. Physico-chemical data were collected every two weeks, and macrobenthos were collected every two months from 10 stations located at various intervals along the lower 60 km (38 mi) of the river until September, 1972 (Fig. 1).

Station 1: Located 4.8 km (3.0 mi) upriver from the mouth and 1.0 km (0.6 mi) below the confluence of the Star Lake and Gulf States Canals. Star Lake Canal carried petrochemical effluents from several industries. Gulf States Canal carried cooling water from the Gulf States Utilities generating plant.

Station 2: Located 7.3 km (4.5 mi) above river mouth and 1.3 km (0.9 mi) above confluence of Star Lake and Gulf States Canals.

Station 3: Located 22.2 km (14.5 mi) above river mouth and 0.8 km (0.5 mi) below entrance of Mobil Canal which carried oil refinery and chemical plant wastes.

Station 4: Located 23.5 km (15.4 mi) above river mouth and 1.0 km (0.6 mi) above entrance of Mobil Canal.

Station 5: Located 30.3 km (19.8 mi) upriver from mouth adjacent to Beaumont Bethlehem Ship Yard.

Station 6: Located 37.6 km (23.5 mi) upriver from mouth and immediately below the outfall of the Eastex paper mill effluent.

Station 7: Located 39.3 km (24.3 mi) upriver from mouth and 0.9 km (0.5 mi) above Eastex outfall.

Station 8: Located 46.4 km (29 mi) upriver from mouth and 0.5 km (0.3 mi) above the confluence of Pine Island Bayou.

Station 9: Located 58 km (36 mi) upriver from mouth and 1.0 km (0.6 mi) below the site of the Neches River salt water barrier.

Station 10: Located 60 km (38 mi) upriver from mouth and 1.0 km (0.6 mi) above the barrier site.

River width ranged from 230 meters (252 yd) at Station 1 to 130 meters (142 yd) at Station 10. The substrate at Stations 1 through 5 consisted of clay, mud and silt. Characteristic vegetation consisted of salt marsh species. The substrate at Stations 6 through 10 was composed of sand, silt, and organic detritus. Characteristic vegetation consisted of mixed hardwood-pine forest species.

At the Pine Island Bayou collecting site the width was 32 meters (35 yd), the substrate was clay, silt, and organic detritus, and the vegetation consisted of a hardwood-pine forest.

Methods

During each sampling period specific conductance and dissolved oxygen were measured at the surface, and at the deepest depths that benthics were collected. During the 1970, 1971 and 1972 sampling periods, salinity was measured. Conductivity was determined with a Portable Lectro

MHO-Meter, salinity with a refractometer, and dissolved oxygen by the Alsterberg (Azide) modification of the Winkler method (Amer. Public Health Assoc. 1965). Discharge was estimated from records of the U.S. Department of Interior Geological Survey (1972 and 1973) by summing the discharges from the Neches River at Evadale, Village Creek near Kountze, and Pine Island Bayou near Sour Lake.

Benthic macroinvertebrates were collected with a 15.24 cm^2 (6 in^2) Ekman dredge. Ten dredge samples were taken at each station from a transect from the margin to the five meter depth on each side of the river. The samples were preserved in the field with formalin. In the laboratory the samples were washed in a #30 U.S. standard soil sieve, the organisms removed, and preserved in 70% ethanol.

Diversity ($\bar{d}$) was determined by the equation of Margalef (1956) as modified by Patten (1962) and Wilhm and Dorris (1968):

$$\bar{d} = -\Sigma\ (n_i/N)\ \log_2\ (n_i/N)$$

where n_i is the number of individuals of the i^{th} species and N is the total number of individuals of all species. Diversity ($\bar{d}$) was calculated using the program of Wilhm (1970) modified for the CDC computer at Lamar University.

RESULTS AND DISCUSSION

1967

The effects of salt water intrusion, carrying industrial effluents from downriver were evident (Table 1). Dissolved oxygen concentration decreased and specific conductance increased below the barrier. The substrate below the barrier was covered with several centimeters of black silt which had an odor of hydrogen sulfide and oil. Diversity of benthic macroinvertebrates decreased from 3.30 above the barrier to 0.55 below the barrier. Density decreased from 1575 individuals/m^2 above the barrier to 555 individuals/m^2 below the barrier. Species composition above the barrier consisted of 35 taxa representing 18 dipterans, 6 oligochaetes, 4 ephemeropterans, 2 crustaceans, and one each of the orders Hirudinea, Odonata, Coleoptera, Pelecypoda, and Gastropoda. Below the barrier there were two species of dipterans and three species of oligochaetes, all restricted to marginal areas. The decrease in density of pollution tolerant taxa, e.g. *Limnodrilus hoffermeisteri* and *Aulodrilus pigueti*, and the absence of common estuarine species, e. g. *Laeonereis culveri*, *Congeria leucopheata*, found during earlier random collecting indicated the presence of toxic as well as organic wastes.

TABLE 1

Dissolved oxygen, specific conductivity, and community structure of benthic macroinvertebrates above and below the Neches River salt water barrier dam, September, 1967

	Above Barrier		Below Barrier	
	Surface	4 m	Surface	3.3 m
Oxygen (ppm)	8.2	7.1	3.4	0.0
% Sat.	105	89	45	0
S. Conductivity (μmhos/cm)	186	196	6,300	17,600
Total Species	35		5	
Individuals/m^2	1,575		555	
Diversity ($\bar{d}$)	3.30		0.55	

1970

Prior to installation of the Neches River barrier in July, concentrations of dissolved oxygen and conductivity were similar and near saturation above and below the barrier site at surface and bottom (Table 2). Two weeks after installation, dissolved oxygen was present only in the upper two meters of water below the barrier. Stratification of dissolved oxygen also occurred above the barrier, however less than 0.5 m of bottom water had low oxygen concentration. Conductivity and salinity exhibited inverse trends to dissolved oxygen. After removal of the barrier in September, oxygen concentrations, conductivity, and salinity were again similar from surface to bottom, and from above and below the barrier site.

Prior to installation of the barrier, a density of 2,233 individuals/m^2 distributed among 33 taxa were present and diversity ($\overline{d}$) was 2.84 (Table 2, Fig. 2). While the barrier was in place the number of taxa per collection above the barrier ranged from 29 to 30. Below the barrier the number of taxa per collection ranged from nine to twelve. Density ranged from 1,364 to 1,752 individuals/m^2 above the barrier, and from 646 to 753 individuals/m^2 below the barrier. Diversity ranged from 2.91 to 3.03 above the barrier, and from 1.43 to 1.85 below the barrier.

After the barrier was removed the number of taxa collected above the site slightly decreased and density increased, decreasing diversity. Below the barrier site the number of taxa increased and density decreased, increasing diversity (Table 2, Fig. 2).

Prior to installation of the barrier, the dominant organisms were *Limnodrilus hoffmeisteri* (37%), *Aulodrilus pigueti* (29%), *Hexagenia limbata* (8%), and a ceratopogonid in the Palpomyia group (7%). Other taxa present were 16 dipterans, 4 ephemeropterans, 3 oligochaetes, and one each in the orders Nematoda, Crustaces, Megaloptera, Coleoptera. Gastropoda, and Pelecypoda.

TABLE 2

Extremes of dissolved oxygen, specific conductivity, salinity, and community structure of benthic macroinvertebrates above and below the site of the Neches River salt water barrier dam prior to installation, while the barrier was in place, and after removal, June to December, 1970.

	Prior to Installation	Barrier Installed		Barrier Removed	
	Barrier Site	Above	Below	Above	Below
Oxygen (ppm)	6.8–7.8	0–10.3	0–8.0	5.4–8.6	5.8–10.1
% Sat.	85–93	0–142	0–110	70–110	75–110
S. Conductivity (μmhos/cm)	178–185	166–225	181–17,100	160–180	100–177
Salinity (ppt)	0	0–0.5	0–10.45	0–0.5	0–0.5
Total Species	33	29–30	9–12	23–29	12–26
Individuals/m^2	2233	1,364–1,752	646–753	1,550–1,948	355–693
Diversity ($\overline{d}$)	2.84	2.91–3.03	1.43–1.85	2.08–2.71	2.12–3.50

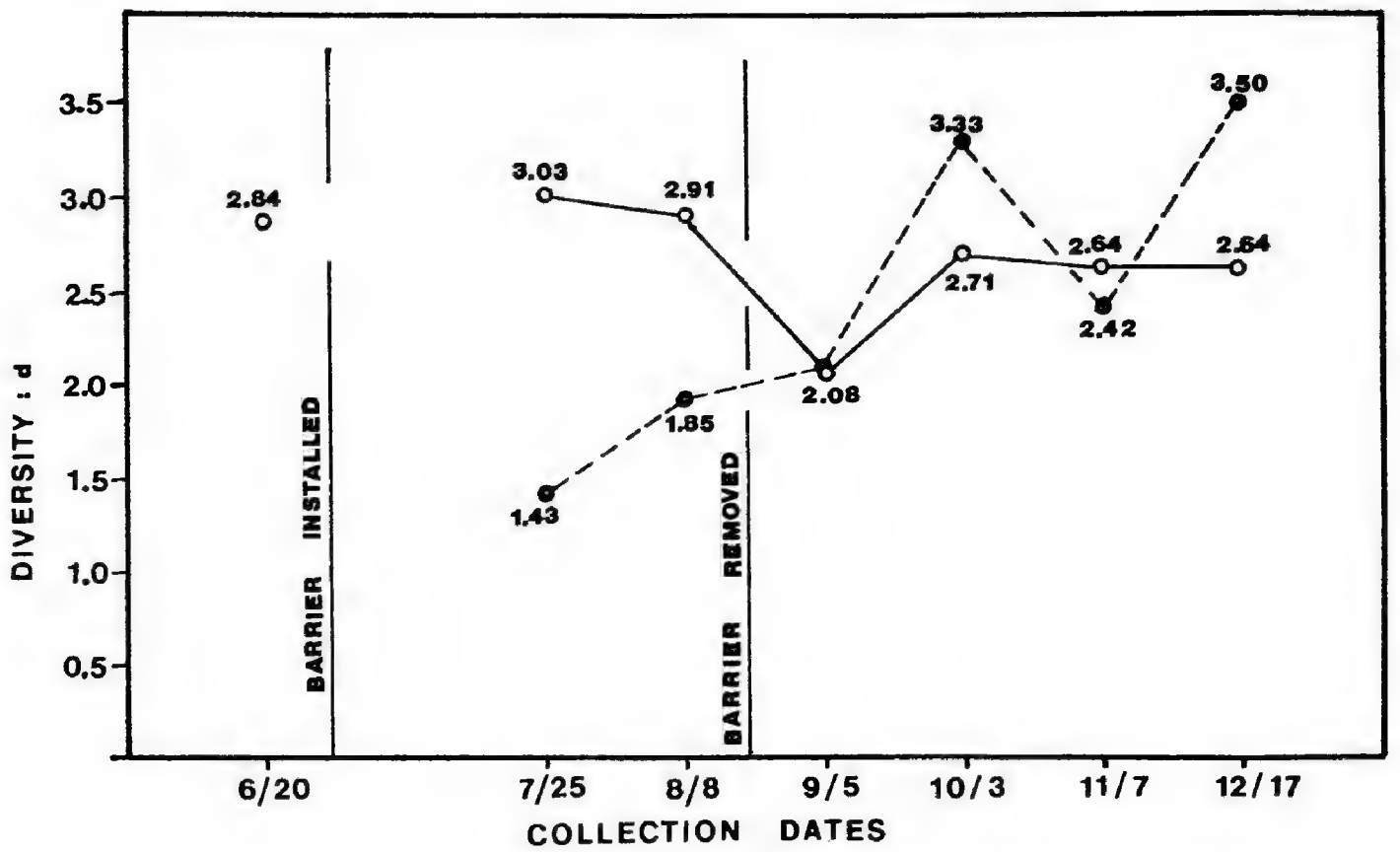

FIG. 2. Diversity $(\overline{d})$ of benthic macroinvertebrates at the barrier site prior to installation and above (○) and below (●) the barrier while it was in place and after removal.

After installation of the barrier *Limnodrilus hoffermeisteri* (57%) and *Chaoborus punctipennis* (34%) formed 91% of the fauna. *Aulodrilus pigueti*, all ephemeropterans, and many chironomids were absent during salt water intrusion. Estuarine species such as *Taphromysis louisianae* and *Corophium lacustre* were restricted to marginal depth. With the exception of an increase in the number of *Chaoborus*, community structure above the barrier was similar before and after installation of the barrier.

After removal of the barrier the dominant organisms on both sides of the barrier site were again *Limnodrilus hoffermeisteri*, *Aulodrilus pigueti*, *Hexagenia limbata*, the Palpomyia group, and several chironomids.

TABLE 3

Dissolved oxygen, specific conductivity, salinity, and community structure of benthic macroinvertebrates above and below the Pine Island Bayou salt water barrier, August, 1970

	Above Barrier			Below Barrier	
	Surface	4 m	5 m	Surface	4 m
Oxygen (ppm)	8.6	5.5	0.0	5.4	0.0
% Sat.	115	67	0	75	0
S. Conductivity (μmhos/cm)	193	215	6,700	6,800	18,000
Salinity (ppt)	0	0	4.4	4.4	11.6
Total Species		17		6	
Individuals/m^2		974		867	
Diversity $(\overline{d})$		1.95		0.37	

Data from the August, 1970 Pine Island Bayou collection indicated degradation of water quality above and below the barrier (Table 3). Salinity data indicated a leakage of the barrier causing anoxic conditions in the bottom meter of water above the barrier. Two meters of water were anoxic below the barrier.

Density of benthic macroinvertebrates was similar above (974 individuals/m^2) and below (867 individuals/m^2) the barrier. However, 17 taxa were present above the barrier and diversity ($\overline{d}$) was 1.95. Six taxa were collected below the barrier and diversity was 0.37. All organisms collected below the barrier were salt water or pollution tolerant taxa. *Chaoborus punctipennis* was the dominant organism at both sites and represented 63% of the total number of individuals above the barrier and 95% below the barrier.

1971–1972

From September, 1971 through November, 1971 the only discharge below the barrier dams was due to effluents entering the river and slight leakage of water over the barriers. Maximum salinity and minimum dissolved oxygen concentrations occurred during this period. Pronounced chemical stratification and anoxic or near anoxic conditions existed at the five-meter depth during this period. In December, 1971, heavy rains washed out the barriers, and a discharge of 197 m^3/sec (6957 cfs) occurred, pushing the salt wedge downriver to Station 2. From December, 1971 through April, 1972 discharge decreased to 102 m^3/sec (3602 cfs), and the salt wedge gradually moved upriver to Station 7. In May, 1972, following spring rains and releases from upriver reservoirs, discharge increased to 206 m^3/sec (7275 cfs) and the salt wedge was again pushed back to Station 2. Discharge then gradually decreased to 51 m^3/sec (1801 cfs) in September, 1972 and salt wedge moved upriver between Stations 8 and 9.

Salinity generally decreased with increased river discharge and increased with distance downriver. Annual extremes of salinity ranged from 1.1 to 20.9 ppt at Station 1, to always less than 0.5 ppt at Station 10 (Table 5).

Dissolved oxygen concentrations generally decreased downriver and were good indicators of water quality. Decreases in oxygen concentration were common at Station 1, due to industrial effluent entering the river from the Star Lake Canal. Other decreases occurred between Stations 3 through 7. The Mobil Canal discharge caused oxygen decreases at Station 3. The Eastex paper mill effluent outfall, located below Station 7, and grain spilled into the river from the Carroll Street loading wharf located between Stations 4 and 5 caused additional decreases.

Ninety-eight taxa of macrobenthos were collected (Table 4). The number of taxa collected at individual stations range from nine at Station 1 to 59 at Station 10 (Table 5). Dominant organisms comprising at least 5% of the total were *Limnodrilus hoffmeisteri* (22%), *Hexagenia limbata* (13%), *Streblospio benedicti* (9%), *Congeria leucophaeta* (6%), *Hypaniola grayi* (6%), and *Polydora* sp. (5%).

Density ranged from zero at Station 3 in October, 1971 when the salt water barrier was in place and the highest concentration of wastes occurred to 1,700/m^2

TABLE 4

Numbers of individual species collected at Neches River Sampling Stations, October, 1971–August, 1972.

Organisms	Stations									
	1	2	3	4	5	6	7	8	9	10
Cnidaria										
Hydra americana	...	...	...	...	...	1	...	...	...	...
Nemertea										
Tubullanus pellucidus	...	3	...	11	19	...	...	...	...	...
Nematoda	...	...	...	...	...	1	2	...	1	4
Annelida										
Oligochaeta										
Limnodrilus hoffmeisteri	38	2	23	3	74	177	101	210	315	685
Aulodrilus pigueti	...	...	...	...	...	...	...	6	8	67
Branchiura sowerbyi	...	...	...	...	...	...	...	3	4	195
Peloscolex sp.	...	...	...	...	...	...	...	...	...	4
Tubifex sp.	...	...	...	...	...	...	...	9	...	1
Dero digitata	...	...	2	...	6	...	2	1	5	6
Pristina sp.	...	...	...	...	...	...	...	...	...	4
Nais sp.	...	...	...	...	...	...	...	...	...	4
Lumbriculus variegatus	...	...	...	...	...	...	...	7	...	1
Eclipidrilus sp.	...	...	...	...	...	...	...	6	2	2
Enchytraeidae	16	12	2	4	2	...	...	...	7	...
Polychaeta										
Nereis succinea	2	21	3	4	1	...	...	...	...	...
Laeonereis culveri	...	...	...	...	...	38	67	145	...	...
Hypaniola grayi	...	...	...	...	68	91	198	91	...	...
Eteone heteropoda	...	2	...	...	...	...	...	...	...	...
Streblospio benedicti	382	161	43	60	1	3	...	...	...	...
Polydora sp.	12	323	41	30	...	...	...	...	...	...
Loandolia fauveli	1	12	1	...	...	...	...	...	...	...
Hirudinea	...	...	...	...	...	...	...	...	1	1
Crustacea										
Mysidacea										
Taphromysis louisianae	1	...	1	...	5	4	8	33	5	7
Isopoda										
Sphaeroma tenebraus	...	...	...	...	...	...	1	...	...	1
Lirceus sp.	...	...	...	...	...	...	...	...	1	...
Idotea montosa	...	3	...	...	...	...	...	...	...	...
Tanaidacea										
Leptochelia dubia	30	1	...	...	...	...	...	...	...	...
Amphipoda										
Corophium lacustre	...	...	...	...	...	21	16	12	7	8
Corophium sp.	...	3	1	...	...	...	...	...	...	...
Gammarus fasciatus	...	...	...	...	1	2	9	1	1	3
Gammarus sp.	...	1	...	1	...	...	...	...	...	...
Melita nitida	...	2	...	...	...	...	...	...	...	...
Cirripedia										
Balanus amphitrite	...	...	...	...	...	...	4	2	...	...
Decapoda										
Neopanope texana	...	1	...	...	1	...	1	...	...	...
Callinectes sapidus	...	1	...	...	...	...	...	...	...	...
Insecta										
Ephemeroptera										
Campsurus sp.	...	...	...	...	...	...	...	...	21	...
Pentagenia sp.	...	...	...	...	...	...	...	...	10	15
Hexagenia limbata	...	...	...	...	10	24	85	276	285	332
Brachycercus sp.	...	...	...	...	...	...	...	...	1	3
Caenis sp.	...	...	...	...	...	...	...	1	3	2
Baetisca lacustris	...	...	...	...	...	...	1	...	1	1
Neocloeon sp.	...	...	...	...	...	...	...	...	4	...
Stenonema sp.	...	...	...	...	...	...	...	...	1	...
Odonata										
Gomphus submedianus	...	...	...	...	1	...	...	3	3	3
Ischnura sp.	...	...	...	...	...	...	...	1	...	...
Trichoptera										
Hydropsyche simulans	...	...	...	...	...	...	...	...	1	...
Coleoptera										
Berosus sp.	...	1	...	...	1	4	3	...	...	...
Dubiraphia sp.	...	...	...	...	...	...	...	2	2	5
Stenelmis sp.	...	...	...	...	...	...	...	...	...	1

TABLE 4—Continued

Diptera										
Chaoborus punctipennis	...	...	...	...	4	15	32	75	38	11
Tanypus sp.	...	...	...	...	1	...	...	2	...	...
Ablabesmyia sp.	...	...	...	...	1	...	...	6	7	15
Procladius sp.	...	...	...	...	3	10	32	20	2	9
Coelotanypus concinnus	...	...	...	...	...	...	...	25	19	19
Clinotanypus sp.	...	...	...	...	...	...	3	13	1	1
Chironomus sp. 1	...	...	...	...	4	138	46	33	23	7
Chironomus sp. 2	...	...	...	...	...	16	...	30	...	1
Chironomus decorus	...	...	...	...	...	1	...	...	...	...
Dicrotendipes nervosus	...	...	...	...	...	...	...	2	4	...
Dicrotendipes sp.	...	...	...	1	6	2	...	17	2	2
Cryptochironomus sp.	...	...	...	...	1	1	9	23	33	59
Cryptochironomus nais	...	...	...	...	...	...	...	...	1	2
Cryptochironomus abortivus	...	...	...	...	...	...	...	...	...	1
Tribelos sp.	...	...	1	1	...	...	...	4	1	2
Goeldichironomus sp.	...	...	...	...	...	...	...	...	...	4
Glyptotendipes sp.	...	...	...	...	...	...	...	...	1	2
Pseudochironomus sp.	...	...	...	...	...	...	...	...	...	1
Polypedilum sp. 1	1	...	...	9	23	45	93	30	94	51
Polypedilum sp. 2	...	...	...	...	...	...	...	7	3	1
Polypedilum sp. 3	...	...	...	...	...	...	...	...	3	...
Polypedilum fallax	...	...	...	...	...	...	...	1	2	...
Polypedilum scalenum	...	...	...	...	...	...	...	1	...	...
Endochironomus sp.	...	...	...	...	...	2	...	...	...	...
Endochironomus tendens	...	...	...	...	...	8	...	4	29	...
Paralauterborniella sp.	...	...	...	...	...	...	...	...	1	...
Stenochironomus sp.	...	...	...	...	...	...	...	1	2	7
Stictochironomus sp.	...	...	...	...	...	...	2	1	6	43
Microtendipes sp.	...	...	...	...	...	...	...	...	1	...
Tanytarsus sp.	...	...	...	...	7	3	...	26	208	9
Micropsectra sp.	...	...	...	...	...	...	1	...	15	3
Diamesa sp.	...	...	...	...	...	...	...	...	1	...
Psectrocladius sp.	...	...	...	...	...	...	5	...	...	...
Metriocnemus sp.	...	...	...	...	...	...	...	...	1	1
Cricotopus sp.	...	...	...	...	1	1	...	...	...	1
Palpomyia group	...	...	...	...	4	...	3	6	19	27
Culicoides sp.	...	...	...	...	...	...	...	1	2	3
Unknown Chironomidae	...	...	...	...	...	1	...	...	1	2
Mollusca										
Gastropoda										
Amnicola sp.	...	...	...	...	...	...	...	...	1	25
Somatagyrus sp.	...	...	...	...	...	...	...	...	1	4
Gyraulus sp.	...	...	...	...	...	...	...	...	1	42
Pelecypoda										
Quadrula apiculata	...	...	...	...	...	...	...	...	...	1
Elliptio sp.	...	...	...	...	...	...	...	...	...	2
Proptera purpurea	...	...	...	...	...	...	...	...	...	3
Leptodea fragilis	...	...	...	...	...	...	...	...	4	1
Sphaerium sp.	...	...	...	...	...	...	...	...	2	24
Musculinum sp.	...	...	...	...	...	...	...	...	3	...
Rangia cuneata	...	...	...	...	...	7	29	60	...	5
Congeria leucophaeta	...	...	...	...	7	157	229	87	7	...

at Station 10 in August 1972, following the longest period of continuous stream flow (Table 5).

Macrobenthic community structure in the lower 30.3 km (19.9 mi) of the river (Stations 1 through 5) was characterized by low densities and numbers of taxa. Extreme changes in salinity and discharge, the presence of pollutional effluences, and the dredged navigation channel made this section of the river a harsh environment for benthic organisms. The benthic community was composed of estuarine and freshwater species during periods of high river discharge. Estuarine species comprised over 50% of the dominant taxa at these stations and maximum densities occurred within the salt wedge when the barriers were not in place.

Community structure above the dredged channel (Stations 6 through 10) was characterized by higher densities and numbers of taxa (Table 5). Freshwater

TABLE 5

Numbers of freshwater, estuarine, and total species, with density and salinity extremes for Neches River stations, September, 1971 to September, 1972

Stations	Freshwater Species	Estuarine Species	Total Species	Densities No./m²	Salinities ppt
1	3	6	9	26–1,691	1.1–20.9
2	4	12	16	159–1,072	1.1–20.3
3	4	6	10	0– 164	<0.5–17.6
4	6	4	10	26– 194	<0.5–17.6
5	16	8	24	34– 461	<0.5–15.9
6	18	8	26	276–1,016	<0.5–15.4
7	16	10	26	426–1,343	<0.5–15.4
8	36	7	43	538–1,339	<0.5–13.2
9	54	4	58	271–1,571	<0.5– 9.9
10	58	1	59	784–1,700	<0.5

species composed over 50% of the fauna at these stations. Only freshwater species were established at Station 10 which was not subject to salt water intrusion. All polychaetes and several crustaceans were present only during periods of salt water intrusion. Conversely, most insects were present only when salinities less than 0.5 ppt occurred.

Rangia cuneata was abundant above km 37.6 (mi 23.5) up to the sites of the salt water barriers, and in Sabine Lake into which the Neches River flows. No clam beds were established below Station 7 and the Eastex paper mill outfall. The absence of *Congeria leucophaeta*, *Hypaniola grayi*, and *Corophium lacustre* below Station 5, in a suitable salinity environment, indicated their sensitivity to pollution.

Diversity ($\bar{d}$) of macrobenthos generally decreased downriver (Fig. 3). Annual diversity increased from 1.19 at Station 1 to 3.89 at Station 8, then decreased to 3.27 at Station 10. Depressed $\bar{d}$ values occurred at Stations 1 through 9 in October, 1971 when the salt water barriers were in place and maximal concentrations of industrial wastes occurred. Zero diversity occurred at Stations 3 and 4 in October and no values above 2.7 were found below the barrier. Elevated $\bar{d}$ values occurred at Stations 1, 2, and 3 in June, 1972 during salt water intrusion. The highest $\bar{d}$ values at Stations 4 and 5 occurred in December, 1971 just after the salt water barriers washed out. Several freshwater species occurred this far downriver for the first time. Elevated $\bar{d}$ values occurred at Stations 6 through 10 when salt water was not present. Depressed $\bar{d}$ values in the upper river were often due to redundancy of non-pollutional or non-salt water tolerant species. Diversity values less than 2.5 occurred at Station 10, which was not subject to pollution or salt water, on three of six collections due to redundancy of *Hexagenia limbata*, *Branchiura sowerbyi*, or some chironomids.

Wilhm and Dorris (1968), using data from many investigators of freshwater and estuaries, reported that $\bar{d}$ values less than 1.0 were common when heavy

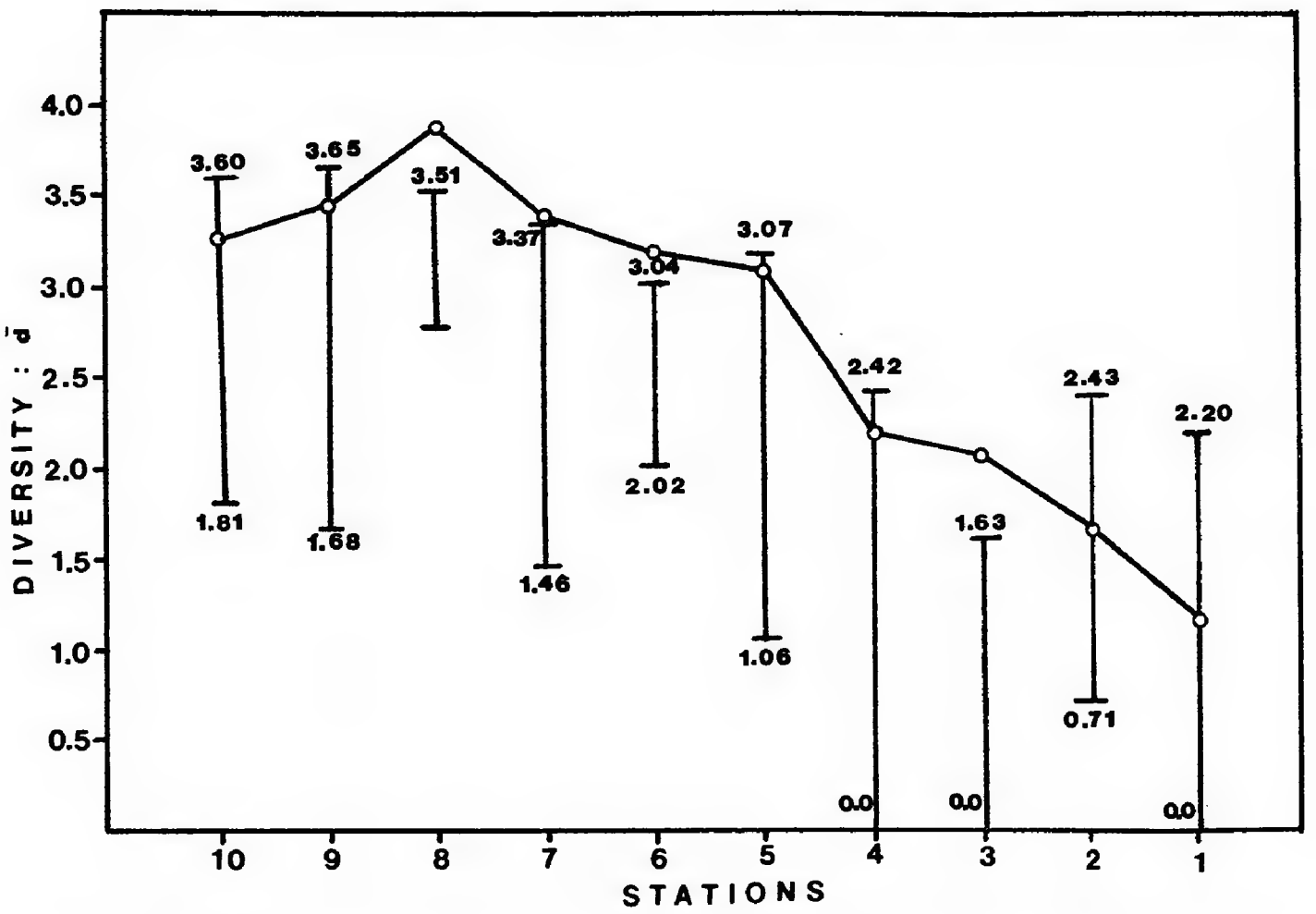

FIG. 3. Benthic macroinvertebrate annual diversities (○) and extremes for Neches River collecting stations, October, 1971–August, 1972.

pollution occurred. Values between 1.0 and 3.0 indicated moderate pollution, and values exceeding 3.0 characterized clean water. However, Holland *et al.* (1973) found that $\bar{d}$ values above 2.5 indicated clean water conditions in Galveston Bay estuary. In the Neches River several values below 2.5 occurred during clean water conditions.

Duncan's multiple range test (Duncan 1955) was performed on the mean annual station $\bar{d}$ values to determine significant difference between stations at the 5% level (Fig. 4). Stations 1 through 4 were not significantly different from each other, and Stations 6 through 10 were not different from each other but were different from Stations 1 through 4. Station 4 was not different from Station 5, and Station 5 was not different from Stations 6 and 7.

Several authors have recently questioned the use of Shannon's diversity index because it depends upon a hypothetical total number of species and must be considered an empirical value (Hurlbert 1971, Peet 1974). The present study shows that caution should be used in making water quality interpretations based only on d values. Diversity values should always be used to complement tabular analysis of taxa distribution and abundance with physio-chemical data, and knowledge of tolerance limits of the organisms involved.

By utilizing salinity gradients, dissolved oxygen concentrations, diversity values, and knowledge of tolerance limits of the organisms involved, it was deter-

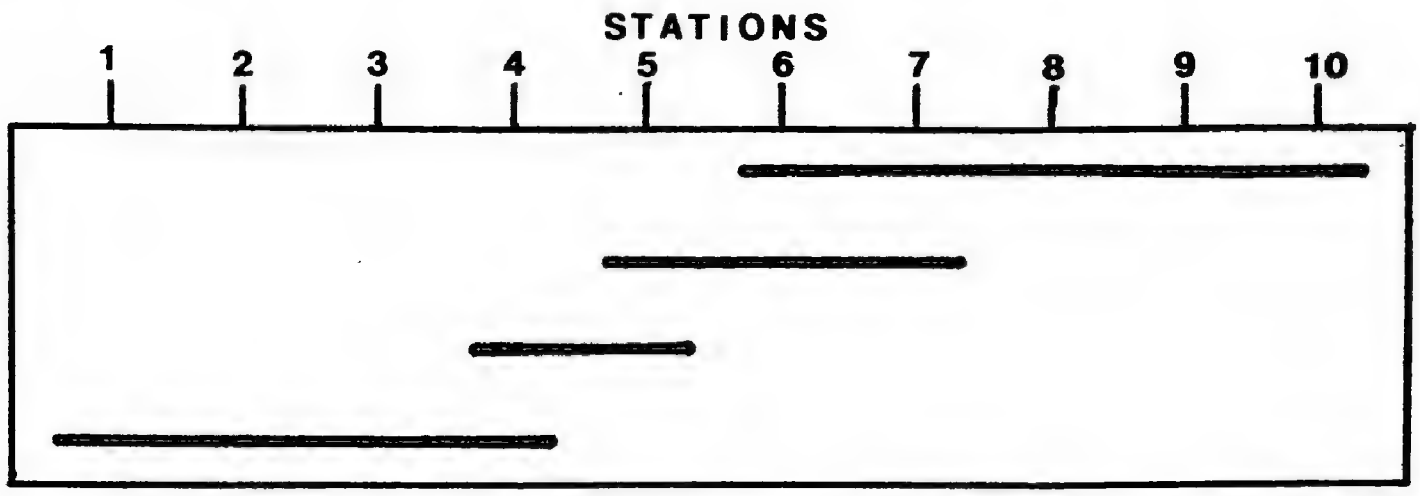

FIG. 4. Duncan's multiple range test on average $\bar{d}$ values. Stations underlined by the same line were not significantly different.

mined that Stations 1 through 5 were subject to heavy to moderate stress and pollution. Stations 6 through 9 were subject to moderate stress to clean water conditions, and Station 10 always had clean water conditions.

The above data seem to indicate that macrobenthic communities in the lower reaches of river in estuaries have higher diversities during periods of salt water intrusion when no concentration of pollutional effluents occurs. The upper reaches of riverine estuaries have higher diversities when freshwater conditions exist. Riverine estuaries are seasonally programmed and very dynamic; thus water quality and the biota constantly change. However, the general trends that existed during this study should be useful in determination of ecological effects of future river development and management practices.

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WESTERN GULF OF MEXICO RECORDS OF *STENONINEREIS MARTINI WESENBERG-LUND* 1958 (POLYCHAETA, NEREIDAE) WITH CONTRIBUTIONS TO ITS HABITAT ECOLOGY

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ABSTRACT

The range of *Stenoninereis martini* is extended from the eastern Gulf of Mexico and eastern Caribbean Sea to include the northwestern Gulf along the Texas coast. Differences and similarities in habitat ecology of the six known localities are presented and discussed.

INTRODUCTION

Stenoninereis martini is a minute aberrant nereid with a reported length to 6 mm, width to 2 mm including setae, and segments to 34 (Pettibone 1971). *Nicon lackeyi* Hartman, 1958, has been referred to *S. martini* (Pettibone 1971). Heretofore, reported occurrences were restricted to synonym type localities and one additional locality, all in the eastern Gulf of Mexico and Caribbean Sea.

Habitat Ecology of Previously Reported Localities

Type locality of *S. martini* is Devils' Hole Swamp, a sinkhole pond about 150 m inland on St. Martin Island, West Indies (Wesenberg-Lund 1958). The pond is subject to tidal movements, has a bottom of rocks with mud, detritus and algae, a pH of about 8 and a relatively constant salinity of 13.8 ppt. Type locality of *N. lackeyi* is Warm Mineral Springs, Sarasota County, Florida, a large inland spring having a constant temperature of 30 C, pH of about 7.2 and salinity of about 17 ppt (Hartman 1958). The water contains hydrogen sulfide but no dissolved oxygen and supports a unique flora and fauna (Lackey 1957). Located approximately 18 km inland, the spring has no direct connection with the Gulf of Mexico.

The relatively constant and unique environmental conditions of Warm Mineral Springs and Devils' Hole Swamp previously suggested that *S. martini* had specific habitat requirements. However, this hypothesis was dispelled when Taylor (1971) reported *S. martini* from open water areas of Tampa Bay, Florida, which is characterized by widely fluctuating environmental conditions.

Occurrence and Habitat Ecology on the Texas Coast

Three anterior portions of *S. martini* were collected by the third author in September 1972 in Cedar Bayou, a small tidal stream in Chambers County, Texas, which empties into upper Galveston Bay. These specimens were compared with topotypes of *N. lackeyi* collected by the second author and determined to be conspecific. It is noted that one topotype exceeded the maximum length of 6 mm reported by Pettibone (1971) by 1.5 mm. Specimens from Cedar Bayou thus represent the first record of *S. martini* in the northwestern Gulf of Mexico. Hydrological parameters measured at time of collection were pH—8.6, salinity—17.2 ppt, dissolved oxygen—3.5 ppm and temperature—30 C. Cedar Bayou is subject to extreme changes in salinity and dissolved oxygen and is relatively polluted by domestic and industrial wastes, thus differing greatly from the nearly constant environmental parameters reported for Warm Mineral Springs and Devils' Hole Swamp.

Dr. J. S. Holland (personal communication) of the Port Aransas Marine Laboratory, The University of Texas Marine Science Institute, recorded 236 individuals of *S. martini* in a study of the Nueces and Corpus Christi Bay systems during November 1972 through May 1975. A single upper Nueces Bay station under direct influence of fresh-water discharge from the Nueces River yielded 216 (92%) of the individuals. Environmental parameters at this station fluctuated greatly, with salinity ranging from 0–32 ppt but normally below 17 ppt. Substrates were soft muds with shell; suspended organic particulate matter was prevalent in the water at this station. The remaining 20 individuals were taken from seven stations, of which two stations exhibited relatively high salinity regimes.

Six specimens were taken by the first author in Crab Lake, Matagorda County, Texas in May and June, 1975. Crab Lake is a small, brackish-water tertiary bay typical of the central and upper Texas coast, and like Cedar Bayou and Nueces Bay is characterized by wide ranges in water temperature, salinity and dissolved oxygen. Bottom substrates were fine muds with high organic content derived from surrounding *Spartina alterniflora* marsh.

DISCUSSION

The occurrence of *S. martini* in Texas coastal waters extends its known range from the eastern to the northwestern Gulf of Mexico. It is apparent that in Texas waters *S. martini* has an affinity for soft substrates of high organic content in upper estuarine areas under direct influence of fresh-water runoff. Most Texas localities appear to be stressed with regard to salinity, temperature and dissolved oxygen due to natural and/or altered characteristics. In this respect the habitat ecology of *S. martini* in the northwestern Gulf of Mexico is similar to that reported by Taylor (1971) in Tampa Bay but very different from the nearly constant conditions of Warm Mineral Springs and Devils' Hole Swamp.

The fact that known localities of *S. martini* are in three widely distributed areas suggests that *S. martini* probably occurs throughout the Gulf of Mexico and

Caribbean Sea. This is strengthened by the occurrence of *S. martini* in localities relatively close to each other and typified by a habitat type which exists throughout the coastal waters of most of the Gulf and Caribbean.

Recent records of *S. martini* have probably resulted from initiation of benthic sampling in upper estuarine areas. Prior to the early 1970's taxonomically adequate works on Gulf Coast polychaetes were few and works stressing areas similar to Texas localities given here were even fewer. The authors believe that due to its minute size, *S. martini* can be easily confused with juveniles of other nereid species by inexperienced workers, and it has likely been reported as such. However, readily discernible ceratophores bearing terminal cirri are present dorsally on the parapodia of *S. martini* and quickly distinguish it from juveniles of other nereid species.

ACKNOWLEDGMENTS

We are grateful to Dr. Marian Pettibone for verification of specimens from Cedar Bayou and Dr. Wilburn Cockrell and Mr. William Royal for assistance in collecting topotypes at Warm Mineral Springs, Florida. Financial support was received in the form of a grant from Houston Lighting and Power Company administered through the Department of Wildlife and Fisheries Sciences and the Texas Agricultural Experiment Station (TAES Project 1774), Texas A&M University and through additional funding from Houston Lighting and Power Company, Central Power and Light Company of Corpus Christi, City Public Service Board of San Antonio and the City of Austin to NUS Corporation. We acknowledge Drs. D. E. Harper, J. L. Taylor, W. J. Wardle and Ms. N. J. Maciolek for their review of the manuscript.

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A SURVEY OF GAMMARID AMPHIPODS OF THE BARATARIA BAY, LOUISIANA REGION[1]

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ABSTRACT

Because of the limited research dealing with the gammarid amphipod fauna in the Gulf of Mexico, and in the Louisiana delta regions in particular, a study was initiated to investigate the species composition, distribution, and ecology of the indigenous amphipod fauna of the Barataria Bay area.

Specific stations, one in each of five study areas representing varying marsh types and salinity regimes, were established and sampled at approximately monthly intervals. Fifty supplemental stations were also occupied throughout the study areas. Methods of collecting included beam trawl, bottom grabs, dipnets, otter trawls, core samples, and examination of marsh grasses and algae by hand.

Twenty-one species of amphipods were found of which five species and one genus appear to be new to science. Largest populations of amphipods were found in the Caminada chenier marsh (old beach ridges), as epifaunal components in and among submerged root systems of eroded stands of *Distichlis spicata*.

Beam trawl samples in the winter months were dominated by amphipods whereas those of late spring and summer were abundant with two species of mysid shrimp.

Analysis of stomach contents of several species of fish in the area revealed *Grandidierella bonnieroides* Stephenson, *Corophium louisianum* Shoemaker, and *Ampelisea abdita* Mills to be the most frequently encountered amphipods.

INTRODUCTION

The purpose of this paper is to present an initial survey of the gammarid amphipod fauna in Louisiana marshes. This study is intended primarily to present facts concerning the ecology and distribution patterns of a unique assemblage of organisms in the Louisiana delta regions.

Some readers may find fault with the number of species presented as undescribed or new to science and yet not described in the paper itself. Except for the new species of *Cerapus*, all other species have been recognized previously and descriptions are in preparation by various specialists throughout the country. It is through courtesy to my co-workers that these descriptions are not presented in

this paper; however, there is adequate descriptive information presented to enable new species to be recognized when descriptions are published. I feel that the information contained in this paper is of sufficient interest and value to publish at the present rather than wait for descriptions which may take several years to reach print.

MATERIALS AND METHODS

Amphipods were collected by several methods, the most common being a 2 m wide 0.5 mm mesh beam trawl. Sampling trips were taken at approximately monthly intervals from March 1974 to February 1975. Additional collecting methods included a 3 m wide 5 mm mesh otter trawl, bottom grab, dipnet, core-sampler, and analysis of various types of marsh vegetation. Floating and submerged vegetation and the root systems of streamside vegetation were examined and sorted by hand. Supralittoral drifts were also examined for the presence of intertide amphipods. Standard 5 m tows perpendicular to shore were made at each of the stations sampled monthly to obtain information on species composition. Fish captured in the beam and otter trawls were identified and measured, and the stomach contents were examined for amphipods.

The study area was located approximately in the western portion of the Barataria Bay complex in St. John the Baptist and Lafourche Parishes (Fig. 1). Samples were also taken from the Lac Des Allemands and Lake Bouef regions in the northern part of the Barataria drainage basin.

Water depths in the study area averaged 0.5 m and were never deeper than 1.5 m, with the exception of some dredge samples and areas where floating vegetation was sampled.

RESULTS

Distribution and ecology of 21 species of the Suborder Gammaridea found in the study area from March 1974 through February 1975 are presented. Five new species and one new genus are discussed. Species identifications were verified by Dr. E. L. Bousfield of the National Museum of Canada. Classification follows that of Barnard (1969).

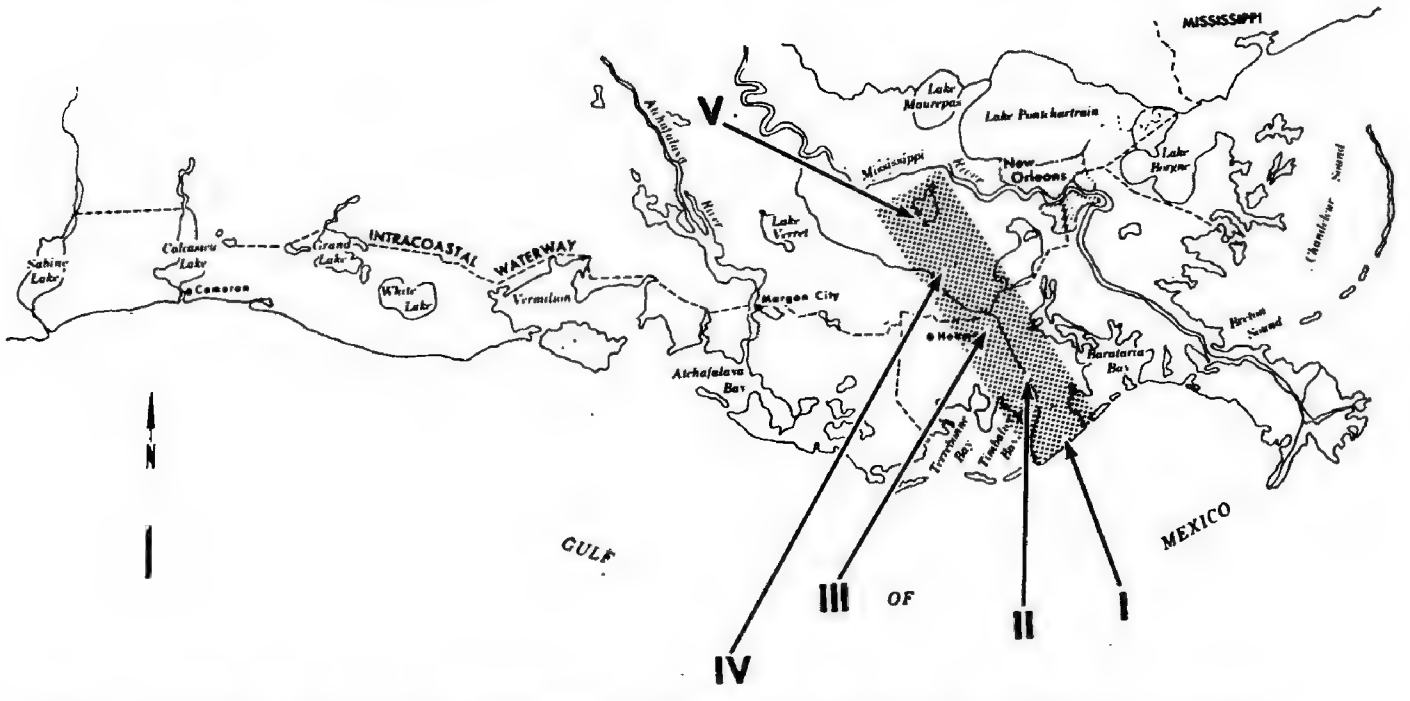

FIG. 1. Location of research (stippled) and individual study sites (roman numerals).

Epifaunal Genera

Genera in this category inhabit or nestle among various epiphytic plants and animals. Epifaunal genera are further divided into tube builders and none-tube builders (burrowers).

Tube-builders

Family: Corophiidae

Corophium louisianum Shoemaker 1934

Distribution: Shoemaker (1934, 1947) listed *C. louisianum* from Chef Menteur, Louisiana; Biloxi, Mississippi; and Sarasota Bay, Florida.

Ecology: *C. louisianum* was recorded from all stations at all times of the year. Tubes of *C. louisianum* were abundant on pilings, submerged tires, along piers, on old oyster shells, and among roots of *Spartina* and *Distichlis*. However, it was seldom taken in beam trawl samples and when present was never farther than 1 m from shore. *C. louisianum* ranged over salinities from 0–30 ppt but most frequently from 10–25 ppt. Other amphipods usually associated with *C. louisianaum* were *Mucrogammarus mucronatus* and *Melita nitida*. Farrell (1970) reported *C. louisianum* as common around oyster reefs and on pieces of driftwood fouled with shipworms.

C. louisianum was frequently encountered in fish stomachs along with *Grandidierella bonnieroides*.

Family: Photidae

Microprotopus shoemakeri Lowry 1974.

Distribution: This species was previously known from its type locality of Cumberland Sound, Fernandina Beach, Florida, and off Rockville, South Carolina (Lowry 1972).

Ecology: Several hundred specimens of this amphipod were collected along beaches after Hurricane Carmen passed through the study area (8 September 1974), probably transported from offshore areas by strong storm action. Subsequent sampling in the near shore area failed to reveal additional specimens. Specimens of *M. shoemakeri* were found clinging to small fragments of wood and other organic matter that had accumulated between ripple marks in the surf zone. The normal substrate preference of *M. shoemakeri* is not known locally. Recently, however, investigations have revealed that *M. shoemakeri* constructs tubes in muddy bottoms exposed to wave action.

Farrell (1970) recorded year-round populations of a related species, *M. raneyi*, in offshore areas of Mississippi.

Non-tube builders (burrowers)

Family: Atylidae

Atylus sp.

Distribution: Barnard (1969) lists 22 species in this genus, cosmopolitan and littoral with two boreal bathyal species.

Ecology: Essentially an oceanic genus, one specimen was found clinging to plant material along with *M. shoemakeri* in the surf zone. Occurrence of this specimen in nearshore waters indicates possible transport by storm action from deeper waters. *Atylus* sp. has been reported in plankton tows from Louisiana marshes by Gillespie (1971) and Juneau (1975). Farrell (1970) lists *Atylus minikoi* Walker, inhabiting grass beds and accumulated debris on the substrate from the Gulf coast of Mississippi.

Family: Crangonycidae

Crangonyx pseudogracilis Bousfield 1973

Distribution: Bousfield (1958) recorded this species from throughout the Mississippi drainage system.

Ecology: *C. pseudogracilis*, a fresh water species, was taken only during the colder months from turbid waters of low pH (5.1) in Lac Des Allemands in the northern part of the study area. It was usually taken among the root systems of the water hyacinth *Eichornia crassipes*.

Crangonyx obliquus Hubricht 1943

Distribution: This species is listed by Hubricht (1943) as occurring from Michigan and Indiana south to Louisiana and Georgia.

Ecology: *C. obliquus* was taken at the same time as *C. pseudogracilis*, however, *C. obliquus* was more common in creeks and ponds while *C. pseudogrocilis* preferred large freshwater lake areas.

Family: Gammaridae

Gammarus tigrinus Sexton 1939

Distribution: Bousfield (1973) lists the range of this species as American endemic; north shore of the Gulf of St. Lawrence south to Chesapeake Bay, and a variety, sporadically south to Florida.

Ecology: *G. tigrinus* was taken in the low salinity areas (less than 5 ppt) typical of the northern parts of the study area. *G. tigrinus* was abundant among the roots of *Eichornia* and among bottom debris where it occurred with *H. azteca* and *Mucrogammarus* sp.

Bousfield (1973) reports *G. tigrinus* from organic debris and *Enteromorpha* clumps in waters with up to 25 ppt salinity. Specimens from Louisiana marshes were never recorded in waters above 5 ppt. salinity, however.

Melita nitida Smith 1873

Distribution: *M. nitida* is found from the southwestern Gulf of St. Lawrence southward to Georgia and Florida and along the Gulf states into Yucatan (Bousfield 1973).

Ecology: *M. nitida* was usually found in shallow muddy waters of intermediate salinity bordering shorelines, associated with various types of epiphytic algae and hydroids where it occurred with *Mucrogammarus mucronatus* and *Corophium*

louisianum. *M. nitida* was also common on pilings, among oyster shells, and along spoil banks covered with *Rangia* shells.

Pearse (1913) reported *M. nitida* from the delta regions of Louisiana, and Farrell (1970) found this amphipod among *Gracilaria* sp. off Deer Island, Mississippi.

Odum (1970) stated that *M. nitida* was a major factor in the conversion of vascular plant detritus to animal protein in the Card Sound estuary in south Florida. Heald (1969) working in conjunction with Odum found that litterbags placed in higher salinities had greater numbers of *M. nitida* than those in lower salinities and that these greater amphipod numbers were accompanied by an accelerated leaf fragmentation rate.

Mucrogammarus (Gammarus) mucronatus Say 1818

Distribution: This species ranges from the Gulf of St. Lawrence south to Florida and the Gulf of Mexico (Bousfield 1973).

Ecology: An abundant species, *M. mucronatus* was taken over a salinity range of 1–30 ppt, but was more common at the middle values. *M. mucronatus* was taken from a number of habitats that supported growths of hydroids and epiphytic algae. In addition, specimens were taken from root masses of *Spartina* and *Distichlis*, pilings, shellbanks, submerged tires along piers, and boat bottoms. Essentially a nearshore species, *M. mucronatus* was usually found in association with *Melita nitida* and *Corophium louisianum*.

Bousfield (1973) listed *G. mucronatus* associated with eelgrass, algal mats, and fouling organisms. In Mississippi waters Farrell (1970) found this amphipod in association with aquatic vegetation, organic debris, and epiphytic algae.

M. mucronatus was found in the stomachs of several species of fish.

Mucrogammarus sp.

Distribution: This undescribed species has been recorded by Farrell (1970) from Mississippi eastward to northern Florida. It is characterized by small size and mucronations more dorsally projected than those of *M. mucronatus*.

Ecology: The ecology is essentially that of *G. tigrinus*. Farrell (1970) found this undescribed species in tidal water areas of very low or no salinity.

Family: Hyalellidae

Hyalella azteca Saussure 1857

Distribution: This species inhabits all permanent fresh waters of North and Central America and Caribbean islands north to the tree line. In coastal areas *H. azteca* occurs in large rivers seaward into tidal fresh water and in fresh water embayments of barrier islands (Bousfield 1958; 1973).

Ecology: Locally, this amphipod occurred in areas of lowest salinity areas (less than 5 ppt) and was recorded in Lac Des Allemands south to areas IV and V. *H. azteca* was found in association with *G. tigrinus* and *Mucrogammarus* species.

Infaunal Amphipods

Genera in this category live in or on the bottom. These forms are divided into tube-builders and non-tube builders (burrowers).

Tube-builders

Family: Ampeliscidae

Ampelisca abdita Mills 1964

Distribution: Mills (1964) gave the range of *A. abdita* as central Main to South Carolina and probably Georgia. The species is also found in the Mississippi delta and along the west coast of Florida.

A. abdita was abundant in the study area where it ranged from the silts of chenier areas north to area III and sporadically into area IV.

Ecology: *A. abdita* constructs shallow tubes in fine silt and mud bottoms. This amphipod was probably much more numerous than indicated by the number of specimens taken. The soft mud tubes of *A. abdita* virtually covered the bottom of many locations and could be found throughout the saline and brackish marsh locations. Collecting inequities were probably due to the use of the beam trawl. Dip net and dredge samples revealed a much greater expanse of *A. abdita* tubes than could be realized from beam trawl samples alone. *A. abdita* was usually taken in large numbers when collected.

Feely and Wass (1971) reported *A. abdita* from the lower Chesapeake, and Farrell (1970) found it common in Mississippi waters. Two congeners of *A. abidita*, *A. verilli*, and *A. holmesi* were reported by Farrell (1970) and Feely and Wass (1971) to occur in sandy substrates, and investigations of such local substrates may reveal the presence of these ampeliscids in Louisiana marshes.

Williams and Bynum (1972) recorded *A. vadorum* and *A. verrilli* as periodically dominant meroplankters in North Carolina estuaries.

Large numbers of *A. abdita* were recorded from fish stomachs at area III.

Family: Corophiidae

Cerapus sp.

Distribution: This species, new to science, is characterized by large size and eight-segmented antennal flagella, currently being described by Thomas and Heard. Barnard (1969) lists five species in this genus. Additional distributional notes from other areas are lacking.

Ecology: *Cerapus* sp. was very abundant in tidal channels of intermediate salinities where its interwoven tubes formed dense mats covering the bottom to depths of 4 m. The tubes of *Cerapus* are composed of detrital material, circular in cross section, and reach 90 mm in length. Specimens in the lab were observed to cut their tubes to 10–15 mm in length and move about when disturbed or in pursuit of food introduced into the aquarium. *A. abidta* was recorded in the same areas as *Cerapus* sp., however, *A. abdita* was usually found in mud while *Cerapus*

preferred silty bottom. Farrell (1970) recorded a similar species, *C. tubularis*, along coastal areas of Mississippi after periods of southerly winds. *C. tubularis* has been recorded from Louisiana water by Gillespie (1971). Juneau (1975) lists *C. tubularis* and *Cerapus* sp. in plankton tows from the Atchafalaya Bay complex.

Grandidierella bonnieroides Stephenson 1948

Distribution: Myers (1970) examined specimens of *G. bonnieroides* from Atlantic and Gulf coasts of Florida to Venezuela and the West Indies.

Ecology: Euryhaline in range (0–30 ppt), *G. bonnieroides* was primarily a benthic amphipod burrowing and constructing tubes in a variety of substrates. It was essentially a shallow water species, never taken in depths of more than 1 meter. It preferred accumulations of particulate *Ruppia*, *Spartina*, and *Distichlis*. *G. bonnieroides* was numerous in the muddy silts and muds of the Caminada chenier complex and in the organic peats in and around area IV. *G. bonnieroides* was common in the shallow flats throughout the interior of the marsh used by wading birds for feeding. Specimens were absent from these areas during the summer months probably resulting from the high water temperatures expected to occur in these shallow pools. Farrell (1970) listed *Grandidierella* sp. associated with *Ruppia* and *Vallisneria*.

This amphipod was the most frequently encountered in fish stomachs. On 28 September 1974 a 0.9 kg ladyfish, *Elops saurus* Linnaeus, was taken from the Caminada chenier in a gill net sample. The contents of the stomach was a 30 mm bolus of amphipods consisting of approximately 175–200 amphipods, all of them being *G. bonnieroides*. Odum (1970) listed *G. bonnieri* (now *G. bonnieroides*; Myers 1970) as the most commonly encountered amphipod in fish stomachs. Farrell (1970) reported *Grandidierella* sp. from stomachs of juvenile sciaenids in Mississippi. Fannaly (Dept. of Marine Sciences, LSU, pers. comm.) found *G. bonnieroides* comprised a large percentage of the diet of adult gobies, pipefish, and juvenile speckled trout associated with growths of *Vallisneria* in Lake Pontchartrain, Louisiana.

Non-tube builders (burrowers)

Family: Amphilochidae

Gitanopsis sp.

Distribution: Barnard (1969) listed 10 cosmopolitan and littoral species in this genus, with two bathyal species to 1096 m.

Ecology: One speciman was taken from a shallow slough along Southwestern Canal near Leeville. However, additional sampling of similar habitats may reveal *Gitanopsis* to be more common than previously believed. *Gitanopsis* is well represented in brackish lagoons and mangrove swamps of the Gulf coast throughout the Caribbean to Trinidad, although virtually nothing has been published to date.

Family: Haustoriidae

Haustorius sp.

Distribution: This apparently undescribed species of *Haustorius* is known only from the Mississippi delta region of the Gulf of Mexico (Bousfield, pers. comm.).

Ecology: This amphipod occurred intertidally from slightly above the drift line to water depths of roughly 1–2 m in depth, in silts and fine sands of passes and exposed as well as protected beaches. Bousfield (1970) reported species of *Haustorius* as almost exclusively intertidal with highly developed filter-feeding mouthparts. *Haustorius* probably obtains nourishment from grazing the rich microflora and fauna from sand grains.

Family: Hyalidae

Parhyale hawaiiensis Dana 1855

Distribution: Shoemaker (1956) found *P. hawaiiensis* widespread along the Atlantic coast of North and South American including the Gulf of Mexico. This species has also been recorded frcm Hawaii, the Galapagos Islands, and the southern coast of California.

Ecology: *P. hawaiiensis* was taken only at areas I and II. This species constructed tunnels through the root systems of *Spartina*. Specimens were also taken from balls of clay in the intertidal zone along the southern portions of Bayou Lafourche. *P. hawaiiensis* showed a preference for the compacted clays that are typical of spoil banks, usually preferring some organic material in the clay matrix such as peats or root systems of marsh grasses.

Family: Oedicerotidae

Synchelidium sp.

Distribution: Barnard (1969) listed seven species and gave their distribution as boreal and littoral to bathyal.

Ecology: The only specimen collected was too small and damaged for positive identification; however, Bousfield (1973) reported a species of *Synchelidium* burrowing in fine sand beaches along semiprotected shores of the Gulf coast.

Family: Talitridae

Orchestia c.f. *costaricana* Stebbing

This species is similar to *O. costaricana* Stebbing 1906, in possessing chelate gnathopods in adult male specimens.

Distribution: Bousfield (pers. comm.) reports the range of this undescribed species as the Gulf coast from the Everglades to Texas.

Ecology: The species occurred in limited numbers with *Orchestia grillus* under accumulated vegetation in the salt marsh but reached its highest numbers in the bases of muskrat houses where it was also taken with *O. grillus*. During periods of high water, the species climbed culms of *Spartina*. Additional field studies are

needed to define the ecology of this species in our locality. Preliminary indications are that it prefers a slightly fresher habitat than that of *O. grillus*. *O. uhleri* Shoemaker, occurs in *Spartina* marshes of western Florida and is presumed to occur in our locality although not collected to date. *O. uhleri* may yet be found in lower brackish portions of Louisiana marshes.

Orchestia grillus Bosc 1802

Distribution: *O. grillus* ranges along the American Atlantic coast, from Chaleur Bay and western Newfoundland south to Florida and the Gulf of Mexico (Bousfield 1973).

Ecology: *O. grillus* is the common intertidal salt marsh amphipod and was found in large numbers throughout *Spartina* and other organic accumulations. *O. grillus* was abundant in the base of muskrat houses with *Orchestia* species A. Pearse (1913) reported *O. grillus* from the margin of Matagorda Bay, Texas.

O. grillus probably represents an important energy pathway in the marsh in terms of converting plant material to animal protein and particulate detritus. Intertidal talitrids can and do consume almost any organic materials within their community. Bowers (1964) kept a species of *Orchestoidea* alive for several months in the laboratory with only moist paper towelling as food. Further research concerning the feeding energetics of this amphipod would allow assessment of its ecological importance in the marsh.

Orchestia platensis Kryer 1845

Distribution: Bousfield (1973) listed *O. platensis* as nearly cosmopolitan along the Atlantic and Pacific coasts. It is found on the American Atlantic coast from southern Newfoundland to Florida, in the West Indies, and in South America to Patagonia.

Ecology: Locally, *O. platensis* was common in the supralittoral area under decaying vegetation and burrowing to a limited extent in the sand. *O. platensis* was more of a beach colonizer than *O. grillus*. It was not unusual to find mixed populations of *O. platensis* and *O. grillus*, but one species always dominated depending on the area. *O. platensis* was more numerous in sandy areas, while *O. grillus* dominated in marsh habitats. Bousfield (1973) listed *O. platensis* as a primary beach colonizer prior to arrival of more specialized talitrids. Pearse (1913) recorded *O. platensis* from Cameron, Louisiana.

Talorchestia sp.

Distribution: This new species is known only from west of the Mississippi delta to Sabine Pass, Texas (Bousfield, pers. comm.).

Ecology: Specimens of *Talorchestia* species were collected in small numbers along barrier and protected beaches where they occurred under the vegetation at MHW level with *O. platensis*. While never numerous, the largest numbers of *Talorchestia* sp. were found along open beaches with fewer specimens taken along protected beaches. In both areas *O. platensis* was the more numerous of the two species.

DISCUSSION

Several authors have stated that amphipods occupy critical levels in detritus-based ecosystems (Darnell 1958, Van Engel and Joseph 1968, Odum 1970). Still, very little is known about the general biology of grammarid amphipods. Barnard (1969) considers our present understanding of amphipod behavior, food habits, and general ecology as rudimentary. The majority of literature dealing with amphipods has been taxonomic to date.

The first published ecological studies pertaining to amphipods (Farrell 1970, Feely and Wass 1971, Watling and Maurer 1972) have illustrated that faunal assemblages differ significantly between coastal regions. As a result, each area must be investigated for its own specific components rather than having broad application of results conducted in geographically removed areas.

Many of the 21 species discussed in this study constitute new records for Louisiana. Five of these represent amphipods undescribed or new to science. They include one each in *Cerapus*, *Orchestia*, *Haustorius*, *Talorchestia*, and *Mucrogammarus*.

The occurrence of *Microprotopus shoemakeri* Lowry constitutes a new record for the Gulf of Mexico. However, since this species was not described until 1972, Farrell's (1970) material of *M. raneyi* should be re-examined.

Pearse (1913) reported 24 species of amphipods from the Gulf of Mexico, three of which were found in this study (*Melita mitida*, *Orchestia grillus*, *O. platensis*). Behre (1950) listed two species of amphipods from the Grand Isle region (*O. platensis* and *Haustoria* [sic] sp.), noting that amphipods were perhaps more numerous than the two records would indicate. Farrell (1970) recorded 31 species of amphipods from coastal and barrier island habitats in Mississippi Sound, six of which were found in this study (*Ampelisca abdita*, *Corophium louisianum*, *Melita nitida*, *Mucrogammarus mucronatus*, *Mucrogammarus* sp., *Orchestia platensis*). No other published studies relating to grammarid amphipods was carried out in the delta region prior to this research. Additional sampling programs will no doubt reveal a much more diverse amphipod fauna, especially in the sandy substrates of coastal bays and barrier island not dealt with in this study.

Seasonal Abundance

Amphipods dominated the beam trawl samples from October through March and were replaced by mysid shrimp from late March through September. These seasonal patterns agree with those discussed by Farrell (1970) but are the reverse of those reported for mysids from Delaware waters by Hopkins (1965). These patterns, however, probably represent apparent and not real populations due to the inadequacy of the beam trawl in sampling the epiphytic regions near shore that contain year-round populations of amphipods.

Distribution

Several distinct groups of amphipods, each occupying a characteristic habitat, were recognizable in the marsh. An epifaunal component along shorelines con-

sisting of *Corophuim louisianum*, *Melita nitida* and *Mucrogrammarus mucronatus*; benthic, tube-dwelling component consisting of *Ampelisca abdita* and *Cerapus* sp.; the burrowers *Grandidierella bonnieroidae* and *Haustorius* sp.; and the intertidal talitrids *Orchestia* sp. A, and *O. grillus*. In the fresher areas only three amphipods were found in any abundance, *Mucrogammarus* sp., *Gammarus tigrinus*, and *Hyalella azteca*. The *Corophium–Melita–Mucrogammarus* complex is abundant in all nearshore areas, dwelling in and among the various epiphytic and epifaunal growths associated with marsh grasses. The *Ampelisca–Cerapus* group inhabited areas of the bottom where there was sufficient tidal flow to supply food for these filter feeders. Of the burrowers, *Haustorius* can be found in large numbers along the swash zone of any sandy beach or pass while *Grandidierella* is ubiquitous in shallow waters of high organic content. The talitrids were numerous throughout the marsh anywhere decaying plant material accumulated. *O. grillus* was also found among *Rangia* shells or under boards and other flotsam transported into the marsh. In the upper reaches of the marsh, accumulations of duckweed (*Lemna*), blown into the shorelines contained thriving populations of *O. grillus* and *Orchestia* sp. A. Amphipods found in the fresh and intermediate marsh areas were usually associated with floating vegetation or on the bottom among organic debris.

Epifaunal forms depend mainly on various types of epiphytic algae (*Polysiphonia* sp. and *Enteromorpha* sp.) and sessile organisms (hydroids and ectoprocts) for habitats. Eroded areas of *Distichlis spicata* possess a thick root mat which provides a favorable attachment for dense growths of various epiphytic forms. The Caminada chenier marsh is composed almost exclusively of *D. spicata* which has eroded to a vertical slope along the shoreline areas, and in which amphipods are abundant. *Spartina patens* in brackish marsh areas yielded fewer numbers and species of amphipods. Fewest species of epifaunal amphipods occurred with *Spartina alterniflora* because of the simple nature of its root system and relatively low numbers of associated epiphytes. These epizoan-epiphytic bands may serve as overwintering areas for amphipods accounting for their great abundance in this area during the colder months; and seasonal fluctuations of these bands undoubtedly affect the amphipods associated with them.

Nagle (1968) found amphipods to be the most abundant macro-organisms inhabiting the epiphytic growths associated with *Zostera* beds. To determine if the epiphytes benefit from this association Nagle conducted a series of experiments with *Zostera* and concluded that grazing by the amphipods were required to keep the epiphytes clean and healthy. Similar experiments with the epiphytes of *Distichlis* are recommended to evaluate the importance of local amphipod-epiphyte relationships.

The intertidal species were divided into marsh and beach forms. Marsh species include *Orchestia* c.f. *costaricana*, *O. grillus*, and *Parhyale hawaiiensis*. The beach forms are represented by *Haustorius* sp., *O. platensis*, and *Talorchestia* species. In terms of total biomass, the marsh-amphipods exceed the beach forms due to the much more extensive habitat and must represent a significant part of the energy cycle of the Gulf coast salt marsh ecosystem.

Transport of amphipods by wind and storm action was recorded twice during the study. In late June of 1974, strong southerly winds for a period of ten days, caused a large accumulation of water hyacinth to be stranded on the northwest shore of Lac Des Allemands (area V). Prior to this, amphipod populations in the area were low with less than 50 specimens recorded. However, samples taken on 27 June indicated an order of magnitude increase in population levels, with *Mucrogammarus* sp., *Hyalella azteca*, and *Gammarus tigrinus* being the species present. The amphipods had evidently been transported from the southern part of the lake system (15 km) among the root systems of *Eichornia*. The dead vegetation then provided a suitable benthic habitat that had two weeks before been a hard-packed clay bottom devoid of any detrital material.

In the southern areas Hurricane Carmen in early September of 1974 brought in *Microprotopus shoemakeri* from offshore habitats and transported the beach dweller, *Orchestra platensis*, northward into area IV, a distance of approximately 20 km. Specimens of *O. platensis* were probably rafted on debris during the storm and deposited with the fall of the water level. After three months, *O. platensis* had disappeared from all area IV stations. Farrell (1970) noted *Cerapus tubularis* and *Microprotopus raneyi* only after periods of strong southerly winds.

Trophic Importance

It is possible that predation plays an important role in controlling the population dynamics of amphipods. High levels of juvenile and subadult fish and invertebrates coincided with low levels of amphipods in the spring, and amphipod levels again rose when animals migrate out of the estuary into the Gulf of Mexico for the winter. Jones (1973) found amphipod tubes themselves to be a potential high-protein food source and found they were consumed in significant amounts by juvenile and adult brown shrimp in the Barataria Bay area. The tubes of *Cerapus* and *Ampelisca* cover extensive areas of the marsh and may represent an important link in estuarine food webs not previously realized.

Movement

Various authors have noticed that some benthic amphipods carry out nocturnal migrations, appearing on the surface at night (Russell 1925, Watkin 1939, Fish and Preece 1970). Williams and Bynum (1972) recorded large numbers of amphipods nocturnally from North Carolina estuaries, at times exceeding in biomass the permanent plankters in the water column. Among the dominant species were two ampeliscids, *A. vadorum* and *A. verrilli*. Mills (1967) found large numbers of ampeliscids at night under full moon and speculated from length-frequency data that swimming peaks occurred at 20–30 day intervals, perhaps correlated with the lunar cycle. In an unpublished study of the Airplane Lake section of the Barataria estuary, Dr. Harry J. Bennett and coworkers periodically found large numbers of ampeliscids taken in tide traps. It would seem advantageous for tubiculous amphipods to carry out reproduction in the water column where males and females would have direct access to one another. Although no night samples were taken during this study, large numbers of

amphipods taken from sheepshead stomachs (*Archosargus probatocephalus* Walbaum) at area III indicate aggregation in the water column. The sole contents of each of the three stomachs consisted of 200–400 specimens of *A. abdita.* No detritus, tube remains, or bottom sediments were present, which would be expected if the amphipods had been taken from their normal habitat. In addition, it would seem difficult for a fish weighing several kilograms to capture a large number of a single small species as *A. abdita* unless the amphipods were numerous in the water column.

CONCLUSIONS

Gammarid amphipods were shown to be a dominant benthic component of Louisiana estuaries. Both infaunal and epifaunal forms contribute type to this dominance.

In order to fully evaluate the unique ecological role played by dominant species of gammarid amphipods in Louisiana's delta system further study is indicated.

ACKNOWLEDGMENTS

I would like to express my sincere thanks to Dr. Bousfield of the National Museum of Natural Sciences, Canada, whose commentary and critical review of the manuscript aided greatly in its preparation.

This investigation was supported cooperatively by funds from Louisiana Offshore Oil Port, Inc. and the Louisiana Sea Grant Program, a part of the National Sea Grant Program maintained by NOAA, U.S. Department of Commerce.

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CALANOID COPEPODS OF THE GENUS *EUCHIRELLA* FROM THE GULF OF MEXICO

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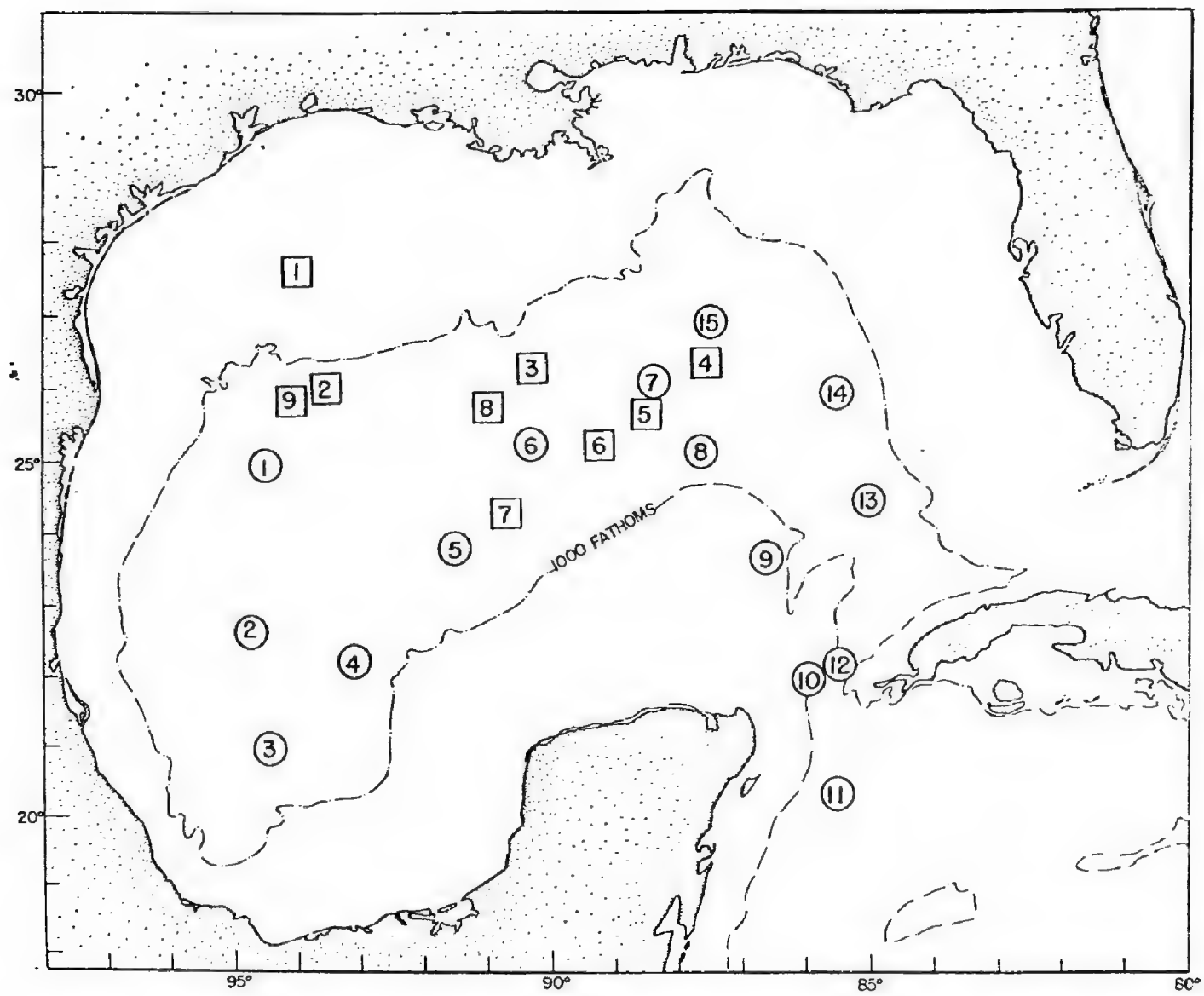
ABSTRACT

During the examination of a total of 93 zooplankton tows taken from various depth ranges between the surface and a depth of about 3000 m in the Gulf of Mexico, 5622 specimens belonging to 9 *Euchirella* species were found. On the basis of these specimens, each species is characterized with pertinent descriptions and illustrations for its easy identification. The relative abundance and bathymetrical distribution of each species by day and night are briefly discussed. A key to the species is given.

Vervoort (1963) reviewed briefly the genus *Euchirella*, recognizing 19 species including a new species, *E. splendens*, which he described in the same paper. One of these 19 species (*E. propria* Esterly) has subsequently been placed in synonymy (Park 1968) and the following 6 new species have since been described: *E. tanseii* Omori, 1965; *E. unispina* Park, 1968; *E. speciosa* Grice and Hulsemann, 1968; *E. acuta* Tanaka and Omori, 1969; *E. pseudotruncata* Park, 1975; and *E. pseudopulchra* Park, 1976. Tanaka and Omori (1969b) recognized that their new species *E. acuta* is synonymous with *E. unispina* Park. *E. grandicornis* Wilson, 1950, a species not included in Vervoort's (1963) review, has recently been redescribed as a valid species by Tanaka and Omori (1969a) from Wilson's original specimens. Therefore, the genus now comprises a total of 24 recognizable species. Of these 24 species, the following 10 species have so far been known to occur in the Gulf of Mexico (Owre and Foyo 1967, Grice 1969, Park 1975): *E. amoena*, *E. bitumida*, *E. curticauda*, *E. maxima*, *E. messinensis*, *E. pseudotruncata*, *E. pulchra*, *E. rostrata*, *E. venusta*, and *E. splendens*. The Gulf of Mexico population recorded as *E. truncata* by Grice (1969) has recently been recognized (Park 1975) as a new species (*E. pseudotruncata*).

In an extensive faunistic study based on a total of 93 zooplankton tows taken on the R/V *Alaminos* in 1971–1972 from various depth ranges between the surface and a depth of about 3000 m in the Gulf of Mexico (Map 1, Table 1), all the previously known species of *Euchirella* have been found except *E. venusta*. This species has been known mainly from the Pacific (Tanaka and Omori 1969a) and its record by Owre and Foyo (1967) from the Florida Current, which is based on a single female specimen, may be a misidentification. Judging from the extent of



MAP 1. Stations where plankton samples were collected during *Alaminos* cruises 71-A-10 (square) and 72-A-10 (circle).

the area covered and the number of samples examined, it is believed that the species found in the present study represent about the entire fauna of the genus *Euchirella* in the Gulf of Mexico. As all the species were represented by both the female and the male, detailed morphological comparisons among the species were possible, leading to an accurate characterization of each species. Since the species descriptions available in the literature are not adequate, particularly for the males, the present paper is intended to provide pertinent systematic accounts of the species including descriptions and illustrations of the diagnostic characters and notes on the abundance and bathymetrical distribution.

The samples were collected mainly with Bongo nets of 70 cm diameter with an opening-closing mechanism operated by messengers. Either 363 or 505 μm mesh nets were used. The tows were made either horizontally at a specific depth or obliquely between the surface and a desired depth. In addition, a number of samples were collected obliquely with a standard one-meter net of 571 μm mesh. The sampling depth was determined from the wire angle and the length of wire out. For certain deep tows, however, a pinger was used to determine the sampling

TABLE 1

Collection data and number of specimens found
(Two samples from the paired Bongo nets are combined)

Station	Sampling depth (m)	Latitude (N)	Longitude (W)	Date	Local time	Bongo net (B) or one-meter net (M)	*E. amoena*	*E. bitumida*	*E. curti-cauda*	*E. maxima*	*E. messi-nensis*	*E. pseudo-truncata*	*E. pulchra*	*E. rostrata*	*E. splendens*
Alaminos Cruise 71-A-10 (September 4–12, 1971)															
1	200	27°42′	94°01′	4/9	19:46–20:18	B							1		
2	200	25°55′	93°30′	5	14:10–15:06	B						3			6
2	500	25°58′	93°33′	5	12:22–13:20	B							18		2
2	1000	26°05′	93°38′	5	08:47–09:47	B					2		28		1
3	200	26°19′	90°20′	6	14:24–15:24	B						11		1	12
3	500	26°24′	90°15′	6	16:30–17:31	B	4			1	12	1	9		3
3	1000–0	26°17′	90°13′	6	18:58–20:55	B	3		5		1		24	2	5
4	500–0	26°22′	87°48′	7–8	23:24–01:05	B	3	2	2		3	1	10		1
4	1000–0	26°28′	87°32′	7	14:14–16:10	B		1	2		10		12		1
4	2000	26°25′	87°33′	7	18:06–20:02	B	1		1						1
5	200	25°50′	88°25′	8	13:01–13:58	B									3
5	500	25°48′	88°25′	8	14:47–15:46	B									
5	1000	25°41′	88°24′	8	17:06–18:19	B	1		1			1	4		
6	200	25°15′	89°11′	9	21:18–22:18	B						1			
6	500	25°15′	89°12′	9	19:22–20:20	B			1		8	6	12		8
6	2000–1000	25°16′	89°16′	9	15:32–17:39	B	3		2			1	6		6
7	500–0	24°22′	90°50′	10	17:11–19:07	M	1	1	3		14	2	23		6
7	500–0	24°17′	90°34′	10	19:24–21:31	B	4	4	2		3		24		10
8	200–0	25°48′	90°59′	11	20:10–21:35	B			7		1	1	18		9
8	500	25°44′	90°56′	11	18:39–19:33	B		1	5	1	4	2	18		4
8	2000–1000	25°38′	90°51′	11	14:01–16:58	B	12		6		11	1	65		17
9	500–0	25°57′	94°09′	12	17:58–19:51	B	3	4	1			2	79		5
9	2000–1000	25°54′	94°00′	12	14:00–16:53	B	2	2	3		4		66		11

TABLE 1—Continued

Station	Sampling depth (m)	Latitude (N)	Longitude (W)	Date	Local time	Bongo net (B) or one-meter net (M)	*E. amoena*	*E. bitumida*	*E. curti-cauda*	*E. maxima*	*E. messi-nensis*	*E. pseudo-truncata*	*E. pulchra*	*E. rostrata*	*E. splendens*
Alaminos Cruise 72-A-10 (May 28–June 11, 1972)															
1	200	25°20′	94°35′	28/5	13:42–14:40	B						2			6
1	1000–0	25°05′	94°32′	28	18:52–20:38	M	4	3	2		2		17		7
1	1591–0	24°57′	94°30′	28	20:58–23:55	B			1			1	20		3
2	1768–0	22°31′	94°44′	29	19:25–23:25	B	3		3		4	2	54		16
2	2846–0	22°41′	94°42′	29	14:00–19:10	B	3	2	3		7	3	64		6
3	200–0	20°59′	94°42′	30	09:43–11:10	B						23			10
3	500	20°54′	94°28′	30	15:30–17:30	B			1				160		
3	500–0	20°54′	94°28′	30	15:08–17:53	M				1		3	369		4
3	1000	20°58′	94°38′	30	12:03–14:00	B	1		8		8		40		8
3	2130	21°00′	94°20′	30	19:19–22:24	B			3			1			11
3	2130–0	21°00′	94°20′	30	18:20–23:46	M	1	3	6			4	63		13
4	25	22°04′	93°09′	31	12:27–13:27	B									
4	50	22°08′	93°09′	31	14:13–15:13	B									
4	100	22°13′	93°09′	31	16:07–17:07	B	1								
4	100–0	22°27′	93°09′	31	23:00–23:43	M	1	4	6		2		13		4
4	200	22°15′	93°07′	31	18:20–19:20	B						25			2
4	500	22°20′	93°07′	31	20:08–22:08	B			2		2		2	1	
5	1000	24°05′	91°25′	1–2/6	23:12–01:07	B			1		3		48		3
5	1000–0	24°05′	91°25′	1–2	22:34–01:57	M	9	1	6		6	6	156		13
5	2000	23°55′	91°27′	1	18:39–20:40	B	2		1			1	1		6
5	2000–0	23°55′	91°27′	1	17:25–22:07	M	3	3	3		3	2	82	2	21
5	2834	23°45′	91°30′	1	12:02–15:00	B			1			1			3
5	2834–0	23°45′	91°30′	1	10:35–16:50	M	2	2	3		3	5	41		4
6	25	25°08′	90°19′	2	12:53–13:53	B									
6	50	25°10′	90°19′	2	14:22–15:22	B									
6	100	25°15′	90°21′	2	16:05–17:04	B									
6	200	25°20′	90°21′	2	18:04–19:04	B	2					3			8

TABLE 1—Continued

Station	Sampling depth (m)	Latitude (N)	Longitude (W)	Date	Local time	Bongo net (B) or one-meter net (M)	*E. amoena*	*E. bitumida*	*F. curti-cauda*	*E. maxima*	*E. messi-nensis*	*E. pseudo-truncata*	*E. pulchra*	*E. rostrata*	*E. splendens*
6	500	25°25′	90°20′	2	20:07–22:08	B	1	2					2		
6	500–0	25°32′	90°19′	2	23:00–23:53	M	5	1	5		2	3	19		10
7	100–0	26°06′	88°23′	3	22:05–23:30	B	10	4	25		65		16		14
7	100–0	26°06′	88°23′	3	22:05–23:30	M	10	10	23		52		30		10
7	1000	25°42′	88°24′	3	13:23–15:22	B	1	4	17		123		96		23
7	1000–0	25°42′	88°24′	3	12:46–16:10	M	9	6	82		149		140		19
7	2000	25°56′	88°24′	3	17:53–19:53	B							1		
7	2000–0	25°56′	88°24′	3	16:38–21:23	M	12		19		27	1	91		16
8	25	25°02′	87°35′	4	12:33–13:32	B	8								
8	50	25°05′	87°37′	4	13:58–14:57	B	11								
8	100	25°06′	87°35′	4	15:23–16:22	B									
8	200	25°10′	87°35′	4	16:55–18:56	B						29			5
8	500	25°11′	87°37′	4	19:47–21:51	B				1					1
8	500–0	25°15′	87°38′	4	22:35–23:32	M	1		7		6	1	13		
9	200–100	23°37′	86°46′	5	13:56–14:56	B	8					1		1	34
9	500–200	23°40′	86°42′	5	15:36–16:36	B					16	6			9
9	860–500	23°45′	86°35′	5	17:23–19:18	B		1	3		30	1	54	18	9
9	841–0	23°50′	86°28′	5	19:59–22:00	M	2	1	2		12	2	34	13	11
10	25	22°01′	85°59′	6	12:21–13:20	B									
10	50	22°03′	85°57′	6	13:46–14:47	B	18								
10	100	22°03′	85°55′	6	15:15–16:16	B	6								
10	200	22°01′	85°55′	6	16:50–17:50	B						2			
10	500	22°01′	85°55′	6	18:45–20:45	B			8		6		14		5
10	500–0	22°01′	85°55′	6	21:32–22:55	M	3	1	4		9		21		
11	200–0	20°26′	85°29′	7	21:12–21:51	B	3		14		15	1	39		7
11	500–200	20°42′	85°38′	7	11:44–14:23	B					5	5			3
11	1000–500	20°34′	85°31′	7	15:37–18:38	B	6		22		27		44		4

TABLE 1—Continued

Station	Sampling depth (m)	Latitude (N)	Longitude (W)	Date	Local time	Bongo net (B) or one-meter net (M)	*E. amoena*	*E. bitumida*	*E. curti-cauda*	*E. maxima*	*E. messi-nensis*	*E. pseudo-truncata*	*E. pulchra*	*E. rostrata*	*E. splendens*
11	2000–1000	20°19′	85°29′	7–8	23:35–03:00	B	7	2	5		6	1	13		4
11	2000–0	20°19′	85°29′	7–8	22:15–03:55	M	17	2	25		16	3	75		6
11	3000–0	20°05′	85°31′	8	04:35–11:13	B	20		26	1	14	1	50		17
11	3000–0	20°05′	85°31′	8	04:35–11:13	M	17		16	2	16	1	43		12
12	1000–0	22°05′	85°32′	8–9	23:30–03:20	M	22	7	13		59	1	72		12
12	1500–0	22°22′	85°25′	9	03:45–07:55	M	15	2	45		37	6	61		9
13	200–0	24°14′	85°07′	9	18:46–20:13	M	2					9	6		18
13	500–0	24°24′	85°00′	9	20:25–23:20	M	4	8	63		34	9	58	16	8
13	1000–0	24°33′	84°50′	9–10	23:38–02:17	M	3	6	13		72	9	81	51	7
14	200–0	25°51′	85°28′	10	12:10–13:07	M	13							2	
14	500–0	25°57′	85°30′	10	13:21–16:45	M	13					13		2	16
14	1650–0	26°07′	85°30′	10	17:07–20:40	M	9	2	2		9	4	35	2	7
14	1650–0	26°07′	85°30′	10	17:07–20:40	B	8	2	6		9	7	64		13
15	50	26°54′	87°32′	11	13:56–14:58	B	2								
15	200	26°59′	87°30′	11	16:10–18:12	B						2		1	22
15	1000–0	27°10′	87°14′	11	21:43–23:20	M	2	5	5		24	5	10	7	9
					TOTAL		337	99	541	7	953	238	2729	119	599
					%		6.0	1.8	9.6	0.1	17.0	4.2	48.5	2.1	10.7

depth. Entire samples were examined under a dissecting microscope to pick up all specimens of *Euchirella.*

Key to the species of *Euchirella* found in the Gulf of Mexico

Female

1. Forehead with a crest (Fig. 2a, b) 2
   Forehead without a crest (Fig. 1a, b) 4
2. Coxa of fourth leg with a comb of more than 10 spines (Fig. 3g) ..... *E. curticauda*
   Coxa of fourth leg with a single spine (Fig. 2g) 3
3. Posterolateral corners of metasome symmetrically rounded (Fig. 2d, e) ..... *E. bitumida*
   Posterolateral corners of metasome asymmetrically produced (Fig. 4d e) ..... *E. maxima*
4. Coxa of fourth leg with a row of more than 5 short spines (Fig. 1g, 8f) 5
   Coxa of fourth leg with 1 or 2 long spines (Fig. 5g, 6e) 6
5. Coxal spines of fourth leg similar in size ..... *E. amoena*
   Coxal spines of fourth leg gradually decreasing in size posteriorly ..... *E. rostrata*
6. Coxa of fourth leg with a single spine; genital segment only slightly asymmetrical (Fig. 6b) ..... *E. pseudotruncata*
   Coxa of fourth leg with 2 spines; genital segment obviously asymmetrical 7
7. Genital segment with a large lobe on distal margin (Fig. 5c) ..... *E. messinensis*
   Genital segment without such a lobe on distal margin 8
8. Genital segment with a lamelliform protrusion on left side (Fig. 7c) ..... *E. pulchra*
   Genital segment with a tooth-like process on right side (Fig. 9b, c) ..... *E. splendens*

Male

1. Forehead with a crest (Fig. 2h, i) 2
   Forehead without a crest (Fig. 1h, i) 6
2. In fifth pair of legs, left basipod considerably longer than right (Fig. 3j) 3
   In fifth pair of legs, left basipod considerably shorter than right (Fig. 2j) 4
3. Exopod of left fifth leg with a chela of equal fingers (Fig. 3l, m) ..... *E. curticauda*
   Exopod of left fifth leg with a chela of unequal fingers (Fig. 4l) ..... *E. maxima*
4. First exopodal segment of left fifth leg reaching distal end of basis of right leg (Fig. 2j) 5
   First exopodal segment of left fifth leg far short of reaching distal end of basis of right leg (Fig. 7j) ..... *E. pulchra*
5. Endopod of right fifth leg with second tooth-like process located posterior to distal end of first exopodal segment (Fig. 5j) ..... *E. messinensis*
   Endopod of right fifth leg with second tooth-like process located anterior to distal end of first exopodal segment (Fig. 2j) ..... *E. bitumida*
6. In fifth pair of legs, left basipod much longer than right (Fig. 8h) ..... *E. rostrata*
   In fifth pair of legs, left basipod much shorter than right (Fig. 1j) 7
7. In right fifth leg, second exopodal segment about 1/3 length of first (Fig. 1j) ..... *E. amoena*
   In right fifth leg, second exopodal segment at least 2/3 length of first (Fig. 6g) 8
8. First exopodal segment of left fifth leg reaching distal end of basis of right leg (Fig. 9h) ..... *E. splendens*
   First exopodal segment of left fifth leg extending far beyond distal end of basis of right leg (Fig. 6g) ..... *E. pseudotruncata*

EUCHIRELLA AMOENA GIESBRECHT, 1888 (Fig. 1)

The original description of *E. amoena* by Giesbrecht (1888) was based exclusively on a male collected from the equatorial Pacific. *E. brevis* Sars, 1905, described solely from females obtained in the Atlantic has been recognized (Grice 1962) as representing the female sex of *E. amoena.* The species has been

known (either as *E. amoena* or *E. brevis*) to occur widely in the tropical, subtropical, and temperate zones throughout the world oceans (Venvoort 1963). In the Gulf of Mexico, the species has been recorded from the Florida Current (Owre 1962).

Female: Body and prosome lengths based on 33 randomly selected specimens, 3.04–3.72 and 2.48–3.16 mm, respectively. Body ovoid (Fig. 1a). Forehead without a crest. Dorsally, posterolateral corners of metasome squarish (Fig. 1c). Genital segment symmetrical when viewed dorsally, without distinct genital swelling. Endopod of antenna about ⅕ length of exopod (Fig. 1e). Second endopodal segment with a single seta on inner and 3 on outer lobe. Mandible with a large conical process on basis (Fig. 1f). Maxillule with 3 setae on basis, 4 on endopod, 8 on exopod, and 8 on outer lobe. Coxa of fourth leg with a row of 5 or 6 small spines along median side (Fig. 1g).

Male: Body and prosome lengths, 3.08–3.36 and 2.48–2.88 mm, respectively, according to 4 specimens found in the study. Habitus similar to female. Forehead without a crest (Fig. 1h, i). Fifth pair of legs consisting of a poorly developed uniramous left leg and large biramous right leg (Fig. 1j). In left leg, endopod absent; exopod with 3 segments, third segment small, not forming a

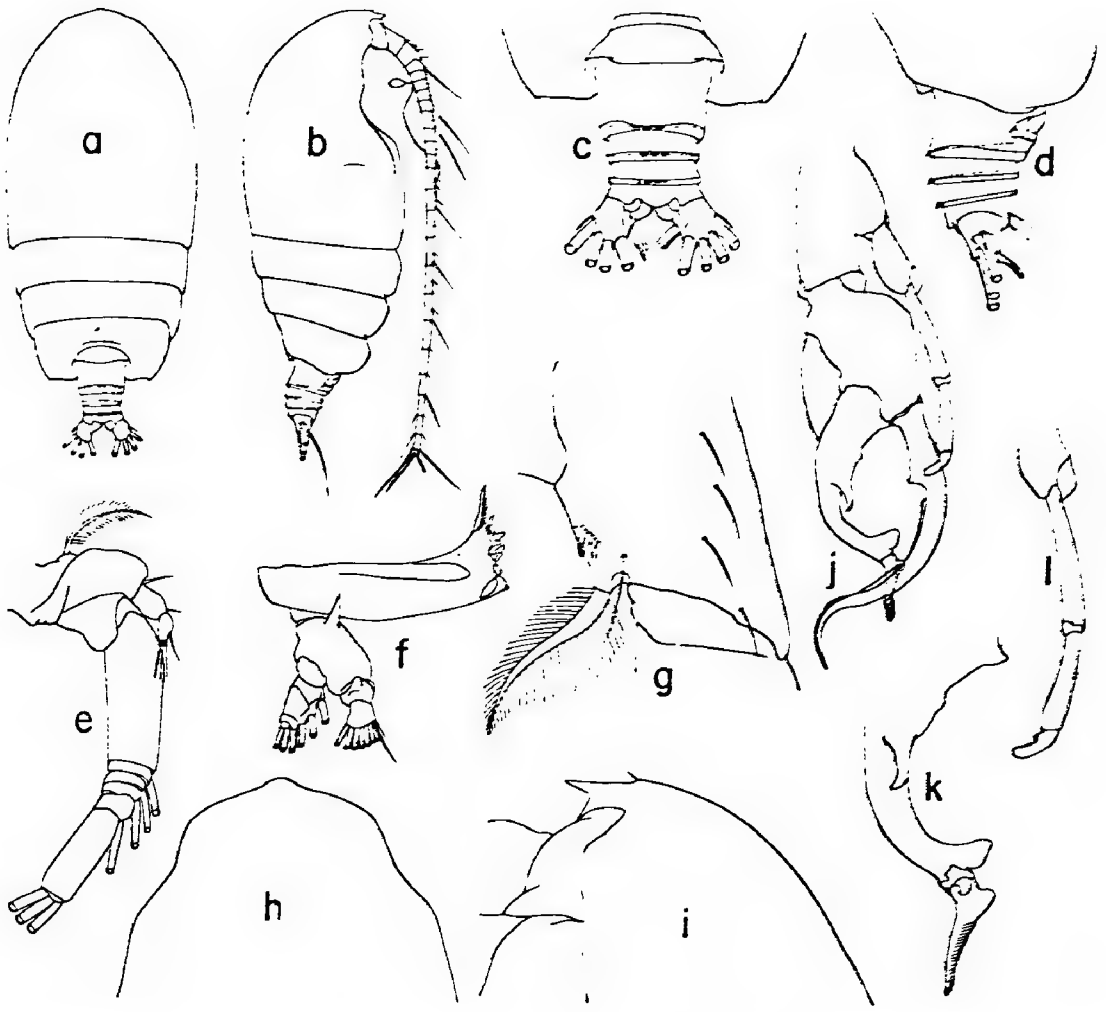


FIG. 1. *Euchirella amoena*. Female: a. habitus, dorsal; b. *item*, lateral; *c*. posterior part of body, dorsal; d. *item*, lateral; e. antenna; f. mandible; g. coxa of fourth leg, posterior. Male: h. forehead, dorsal; i. *item*, lateral; j. fifth pair of legs, anterior; k. exopod of right fifth leg, anterior, l. exopod of left fifth leg, anterior.

chela (Fig. 1l). Right leg with 2-segmented exopod and 1-segmented endopod. Endopod distinctly longer than exopod. First exopodal segment with a large spiniform process midway along inner margin (Fig. 1k). Second exopodal segment about ⅓ length of first.

Occurrence: A total of 337 specimens has been found in this study, which comprised about 6% of all *Euchirella* specimens found in the study. The species occurred throughout the Gulf of Mexico and in all the depth ranges sampled extending from 25 to 2000 m, but no particular depth of concentration was evident. It was the only *Euchirella* species found in the upper 100 m during the daytime.

EUCHIRELLA BITUMIDA WITH, 1915 (Fig. 2)

E. bitumida was originally described by With (1915) from female specimens obtained from the Norwegian Sea. The male was first described by Wilson (1950) from specimens collected in the Philippine Islands region and has been redescribed by Tanaka and Omori (1969a) from specimens obtained in the Izu region of Middle Japan. The species has so far been known to occur widely in the Atlantic, Pacific and Indian oceans (Vervoort 1963, Tanaka and Omori 1969a). In the Gulf of Mexico, it has been recorded by Owre (1962) from the Florida Current.

Female: Body length based on 30 randomly selected specimens, 5.58–6.17 mm. Prosome length, 4.75–5.17 mm. Forehead with a large crest produced anteriorly into a triangular plate when viewed laterally (Fig. 2b). Posterolateral corners of metasome slightly squarish in dorsal view (Fig. 2c), but broadly rounded in lateral view (Fig. 2d, e). Dorsally, genital segment asymmetrical, with a large proturberance on each side of dorsal surface (Fig. 2c). Endopod of antenna about ⅓ length of exopod (Fig. 2f). Inner and outer lobes of second endopodal segment each with 6 setae. First exopodal segment with a tooth-like process on inner margin a little anterior to its middle. Maxillule with 3 setae on basis, 5 on endopod, 11 on exopod and 8 on outer lobe. Coxa of fourth leg with a large spiniform process at base of inner seta (Fig. 2g).

Male: Body and prosome lengths of a single specimen, 5.08 and 4.16 mm, respectively. Forehead with a low crest, more or less triangular when viewed laterally (Fig. 2i). Left fifth leg with a minute endopod (Fig. 2j). First exopodal segment reaching distal end of basis of right leg. Third exopodal segment small, together with distal process of second segment, forming a minute chela (Fig. 2k, l). Right fifth leg with a 2-segmented exopod and 1-segmented endopod. Endopod a little shorter than exopod, with 4 low tooth-like processes along inner margin, 2 anterior and 2 posterior to joint between 2 exopodal segments.

Occurrence: The species was quite rare but occurred throughout the Gulf of Mexico. A total of 99 specimens has been found, which constitute only 1.8% of the total number of *Euchirella* specimens found in this study. During the daytime the species was found only in tows down to depths of 500 to 2846 m, but in the night it was also found in the upper 100 m.

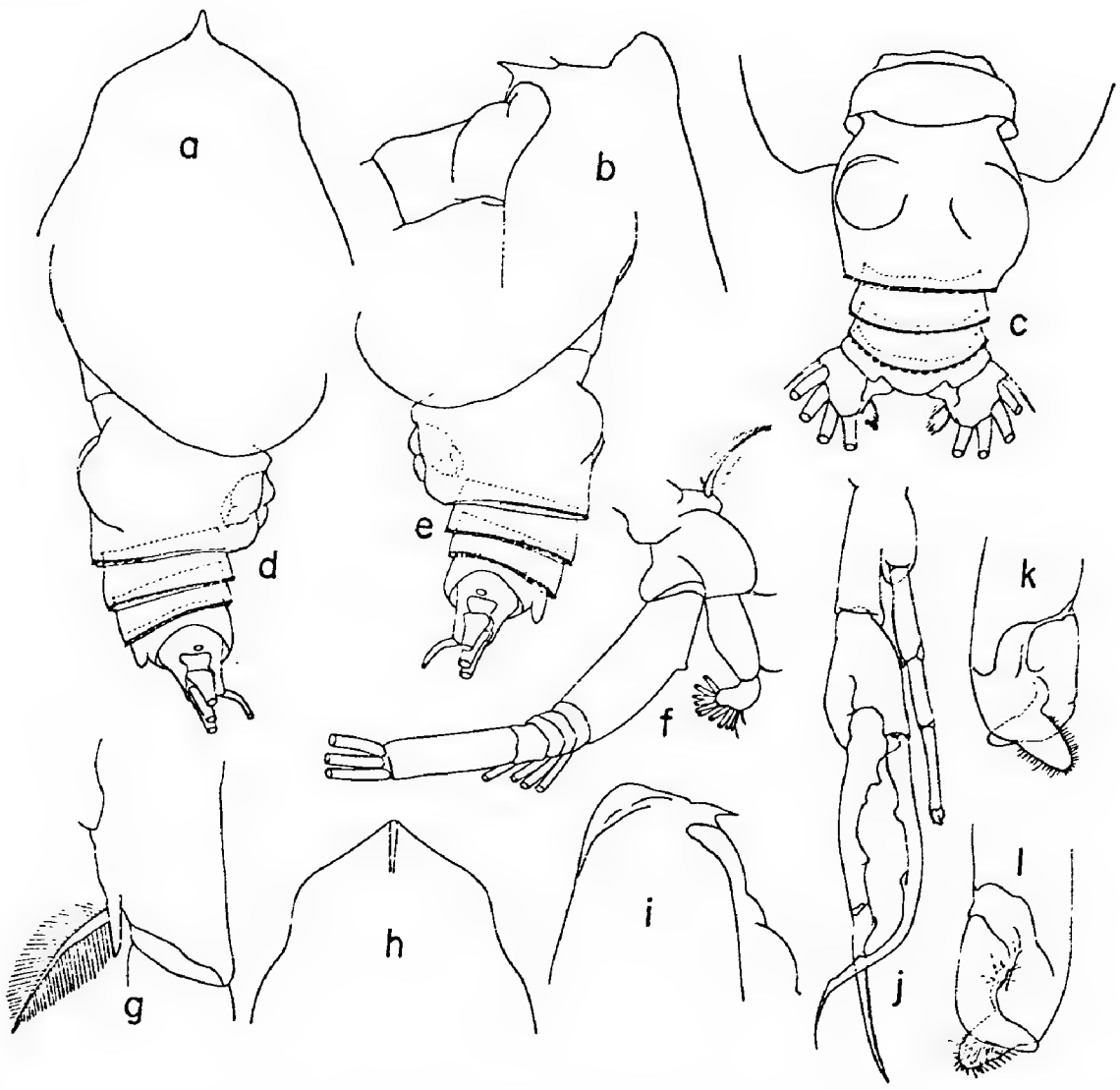


FIG. 2. *Euchirella bitumida*. Female: a. forehead, dorsal; b. *item*, lateral; c. posterior part of body, dorsal; d. *item*, right side; e. *item*, left side; f. antenna; g. coxa of fourth leg, posterior. Male: h. forehead, dorsal; i. *item*, lateral; j. fifth pair of legs, anterior; k. distal part of left fifth leg, anterior; l. *item*, posterior.

EUCHIRELLA CURTICAUDA GIESBRECHT, 1888 (Fig. 3)

Giesbrecht's (1888) original description is based exclusively on the female obtained from deep water in the equatorial Pacific. The male was described for the first time by With (1915) from the Norwegian Sea. As shown by Vervoort (1963) and Tanaka and Omori (1969a), this species has been known to occur widely, though usually in small numbers, in the Atlantic, Pacific, and Indian oceans. In the Gulf of Mexico, the species has been recorded from the Florida Current by Owre (1962).

Female: Body and prosome lengths based on 40 randomly selected specimens, 3.36–3.92 and 3.00–3.48 mm, respectively. Forehead with a large crest. Laterally, crest triangular, with its apex pointing in an anterodorsal direction (Fig. 3b). Rostrum very small. Posterolateral corners of metasome symmetrical, each with a distinct distal part appearing in lateral view like a separate segment (Fig. 3d). Dorsally, genital segment symmetrical, with only slightly swollen lateral sides (Fig. 3c). Genital field produced posteriorly into 3 lobes, clearly visible either laterally (Fig. 3d) or ventrally (Fig. 3e). Third urosomal segment with a conical

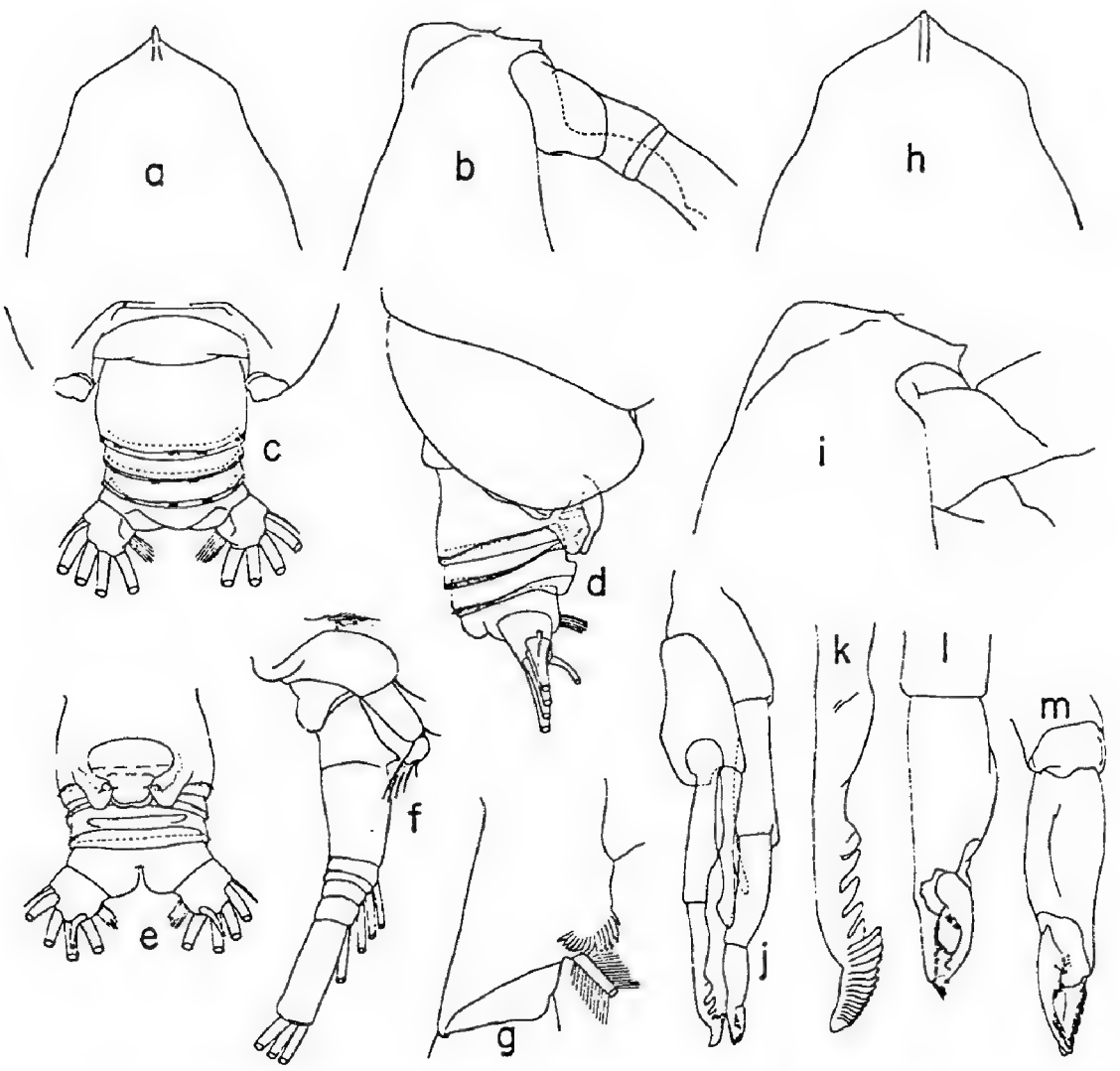


FIG. 3. *Euchirella curticauda*. Female: a. forehead, dorsal; b. *item*, lateral; c. posterior part of body, dorsal; d. *item*, lateral; e. *item*, ventral; f. antenna; g. coxa of fourth leg, posterior. Male: h. forehead, dorsal; i. *item*, lateral; j. fifth pair of legs, anterior; k. distal part of exopod of right fifth leg, anterior; l. distal part of exopod of left fifth leg, anterior; m. *item*, posterior.

process on ventral surface (Fig. 3d). Antenna with small endopod, only about ¼ as long as exopod (Fig. 3f). Second endopodal segment with 2 setae on inner and 3 on outer lobe. Maxillule with 3 setae on basis, 3 on endopod, 11 on exopod, and 8 on outer lobe. Coxa of maxilliped with a conspicuous conical process distally on external margin. Second exopodal segment of second leg with an exceptionally large external spine. Coxa of fourth leg with a comb of about 13 teeth at base of inner seta (Fig. 3g).

Male: Six specimens examined in this study measured 3.44–3.52 mm in body length and 2.64–2.84 mm in prosome length. Habitus similar to female. Forehead with a triangular crest, clearly visible either dorsally (Fig. 3h) or laterally (Fig. 3i). Rostrum small, slightly turned forward. In fifth pair of legs, left basipod much longer than right (Fig. 3j). Left fifth leg with 1-segmented endopod about ½ length of first exopodal segment. Third exopodal segment small, originating subterminally to form a chela together with a long distal process of second segment (Fig. 31, m). Right fifth leg about as long as left leg. Endopod 1-segmented, club-like, with an enlarged distal end, only slightly longer than first exopodal segment. Second exopodal segment in form of a curved spine, with peculiarly serrated distal part (Fig. 3k).

Occurrence: A total of 541 specimens has been found in the study; that is, 9.6% of the *Euchirella* specimens found in the study belonged to this species. The species showed a pronounced diurnal vertical migration. During the daytime, it was taken only in tows down to depths of 500 to 3000 m, with the greatest numbers from a depth range of 1000–500 m. In the night, however, the largest numbers were taken in tows from the upper 100 m. Although more abundant in areas close to Campeche Bank as were the other *Euchirella* species, the species occurred quite regularly throughout the Gulf of Mexico.

EUCHIRELLA MAXIMA WOLFENDEN, 1905 (Fig. 4)

E. maxima was originally described by Wolfenden (1905) from female specimens collected from deep waters of the tropical Atlantic. The male was described by With (1915) from the Norwegian Sea. The species has been known to occur widely in deep waters of the world oceans (Vervoort 1963, Tanaka and Omori 1969a). In the Gulf of Mexico, the species has been recorded from the Florida Current by Owre and Foyo (1964).

Female: Six females found in this study measured 6.92–7.33 mm in body length and 6.08–6.35 mm in prosome length. Forehead with a large crest. Laterally, crest triangular, with its apex pointing in an anterodorsal direction (Fig.

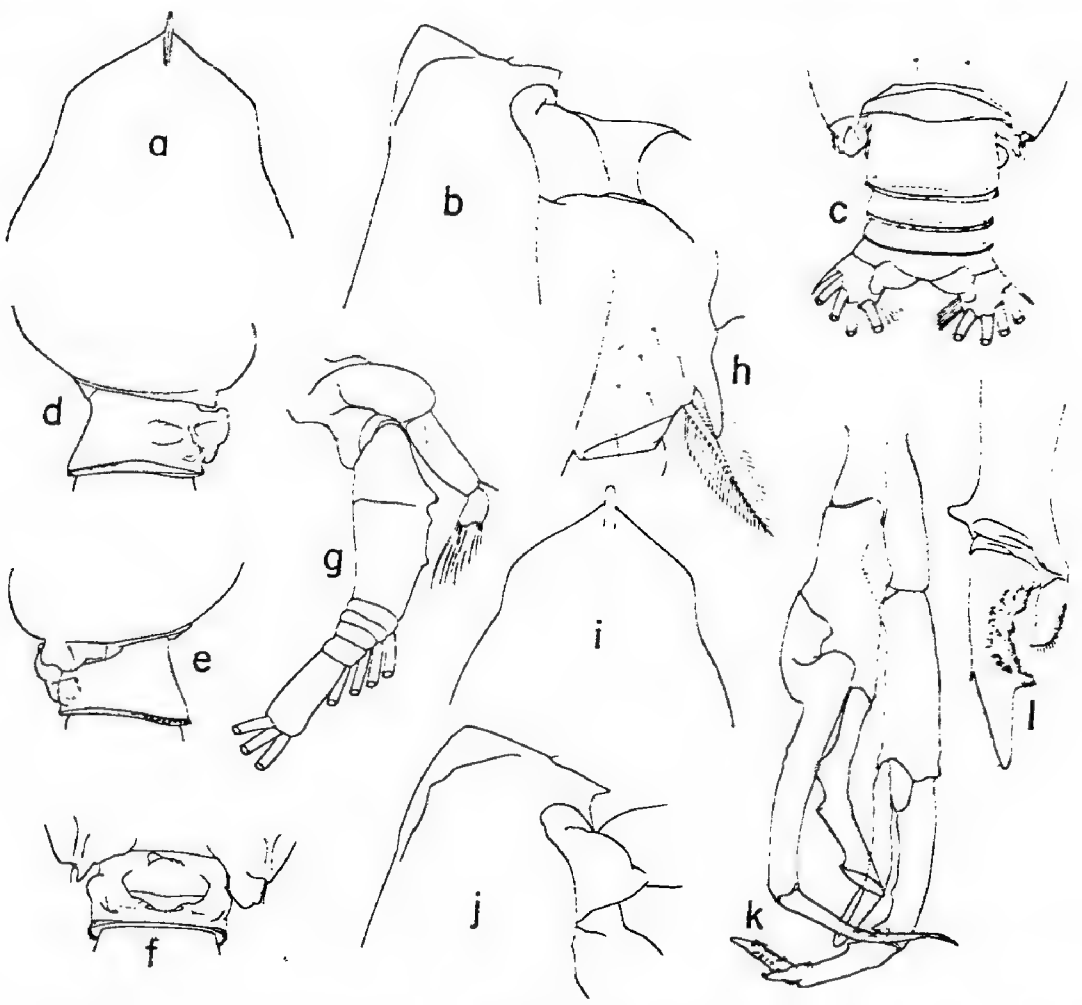


FIG. 4. *Euchirella maxima*. Female: a. forehead, dorsal; b. *item*, lateral; c. posterior part of body, dorsal; d. genital segment, right side; e. *item*, left side; f. *item*, ventral; g. antenna; h. coxa of fourth leg, posterior. Male: i. forehead, dorsal; j. *item*, lateral; k. fifth pair of legs, anterior; l. distal part of exopod of left fifth leg, medial.

4b). Rostrum very small. Posterolateral corners of metasome asymmetrical, each with a lappet of different size and shape (Fig. 4d, e). Dorsally, genital segment symmetrical, with more or less straight sides (Fig. 4c). Ventrally, however, genital segment asymmetrical, bearing a conspicuous swelling of different size at different location on each side and a conical process on anterior side of genital field (Fig. 4f). Laterally, genital field produced anteriorly into a large protuberance (Fig. 4d). Endopod of antenna about ⅓ length of exopod (Fig. 4g). Second endopodal segment with 5 setae each on inner and outer lobes. Maxillule with 3 setae on basis, 3 on endopod, 11 on exopod, and 8 on outer lobe. Second leg with an exceptionally large external spine on second exopodal segment. Coxa of fourth leg with a large spine on inner margin. (Fig. 4h).

Male: A single specimen found in the study measured 6.16 mm in body length and 5.08 mm in prosome length. Forehead with a large crest, triangular in lateral view with its apex pointing anterodorsally (Fig. 4j). Rostrum small but larger than in female. Posterolateral corners of metasome symmetrical, without lappets. In fifth pair of legs (Fig. 4k), left basipod considerably longer than right. Left leg with large, 1-segmented endopod extending beyond distal end of first exopodal segment. Third exopodal segment relatively large, together with a small distal process of second, forming a chela (Fig. 4l). Endopod of right leg 1-segmented, about as long as first exopodal segment, with 2 large conical processes along external margin and blunt distal end. Second exopodal segment tapering in a spiniform process, with distal half of inner margin finely serrated.

Occurrence: *E. maxima* was the rarest species of the genus in the Gulf of Mexico. Altogether, only 7 specimens were found, which comprised 0.1% of all *Euchirella* specimens found in the study. All the specimens were taken in tows down to depths of 500 to 3000 m.

EUCHIRELLA MESSINENSIS (CLAUS, 1863) (Fig. 5)

This species was originally described by Claus (1863) under the name of *Undina messinensis* from the Mediterranean Sea. Giesbrecht (1892) redescribed the species including the male from specimens collected from off Naples. The species has been known to have a wide range of distribution over the Atlantic, Pacific, and Indian oceans (Vervoort 1963). In the Gulf of Mexico, the species has been recorded from the Florida Current by Owre (1962).

Female: Body and prosome lengths based on 60 randomly selected specimens, 4.36–5.25 and 3.58–4.25 mm, respectively. Forehead without a crest (Fig. 5a, b). Rostrum relatively well developed. Posterolateral corners of metasome symmetrical, with smoothly rounded margin (Fig. 5c, d). Dorsally, genital segment asymmetrical, with a large lobe originating from left side of distal margin and extending right over second urosomal segment (Fig. 5c). Endopod of antenna about ¼ length of exopod (Fig. 5f). Two lobes of second endopodal segment each bearing 5 setae. Maxillule with 3 setae on basis, 4 on endopod, 11 on exopod, and 8 on outer lobe. Coxa of fourth leg with 2 large spines at base of inner seta (Fig. 5g).

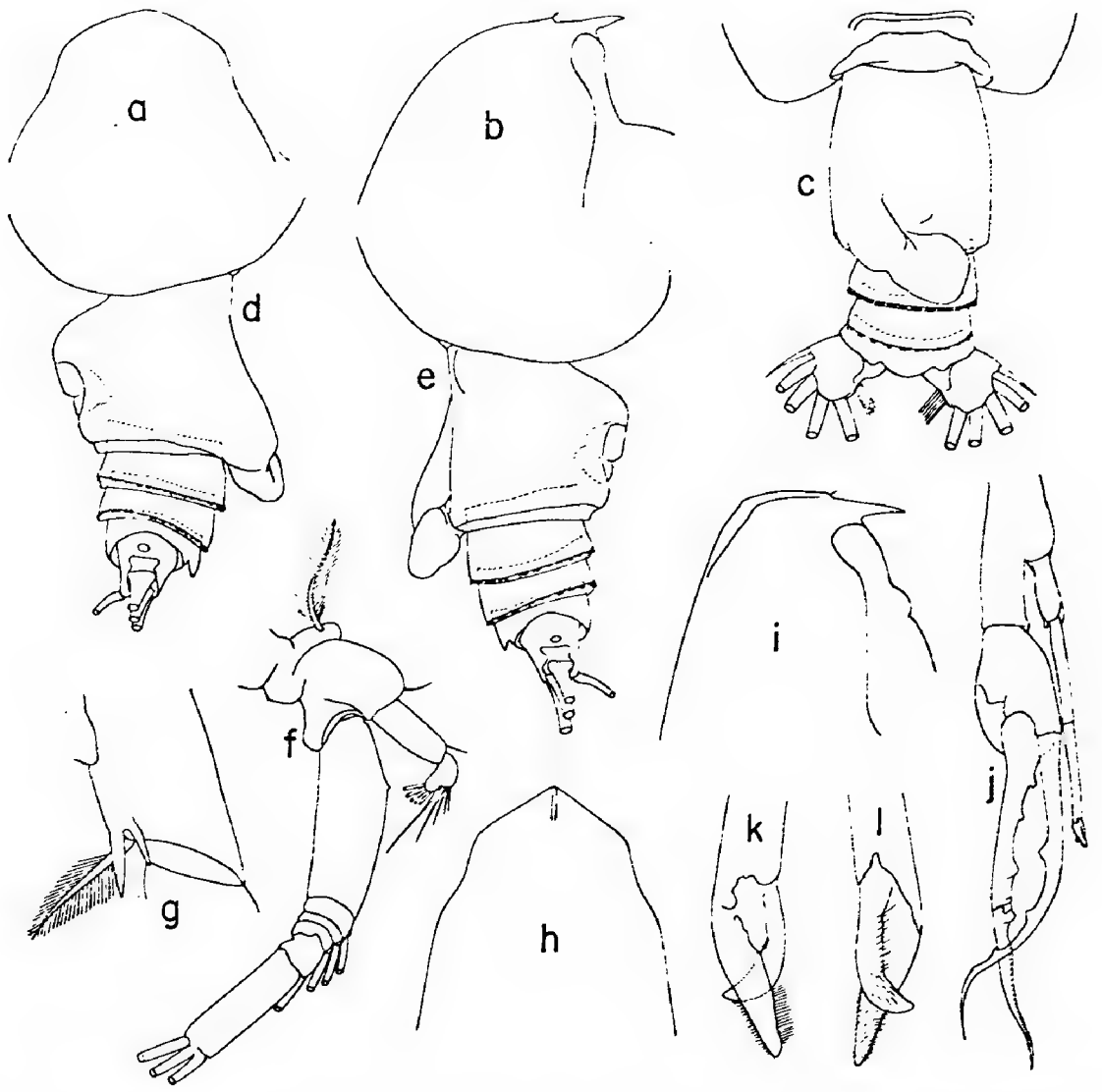


FIG. 5. *Euchirella messinensis*. Female: a. forehead, dorsal; b. *item*, lateral; c. posterior part of body, dorsal; d. *item*, left side; e. *item*, right side; f. antenna; g. coxa of fourth leg, posterior. Male: h. forehead, dorsal; i. *item*, lateral; j. fifth pair of legs, anterior; k. distal part of left fifth leg, anterior; l. *item*, posterior.

Male: Nine specimens examined in the study measured 4.00–4.28 mm in body length and 3.12–3.40 mm in prosome length. Forehead with a low crest (Fig. 5h, i). Rostrum well developed. In fifth pair of legs, left basis reaching distal end of right coxa; first exopodal segment of left leg reaching distal end of basis of right leg (Fig. 5j). Third exopodal segment of left leg small, together with a distal process of second, forming a chela (Fig. 5k, l). Endopod of left leg represented by a minute process. Endopod of right leg with 4 processes along external margin, 1 proximal and 3 distal to joint between first and second exopodal segments (Fig. 5j).

Occurrence: *E. messinensis* was the second most abundant species of the genus in the Gulf of Mexico. A total of 953 specimens was found, which comprised 17% of all *Euchirella* specimens taken in the study. During the day, the species was taken only in tows down to depths of 500 to 2000 m, with the largest catch from a depth of 1000 m. In the night, however, the largest catch was obtained in the upper 100 m. These findings no doubt suggest an extensive diurnal vertical migration of the species.

EUCHIRELLA PSEUDOTRUNCATA PARK, 1975 (Fig. 6)

This species was recently described from the Gulf of Mexico and also found in Sargasso Sea (Park 1975).

Female: According to 30 randomly selected specimens, body and prosome lengths were 4.00–4.66 and 3.20–3.76 mm, respectively. Forehead without a crest (Fig. 6a). Rostrum well developed. Posterolateral corners of metasome symmetrical (Fig. 6b), broadly rounded when viewed laterally (Fig. 6c). Dorsally, genital segment slightly asymmetrical with a low swelling at middle of left side (Fig. 6b). Endopod of antenna (Fig. 6d) well developed, almost ½ as long as exopod. Second endopodal segment with 8 setae on inner and 7 on outer lobe. Maxillule with 3 setae on basis, 5 on endopod, 11 on exopod, and 8 on outer lobe. Coxa of fourth leg with a long, slender spine at base of inner seta (Fig. 6e).

Male: Body and prosome length based on 6 specimens, 3.32–3.80 and 2.72–3.08 mm, respectively. Forehead without a crest (Fig. 6f). Rostrum well developed. Left fifth leg without endopod (Fig. 6g). Third exopodal segment small, together with a round distal process of second, forming a chela (Fig. 6h, i). Distally, third exopodal segment bearing 3 or 4 tooth-like processes. Distal process of second exopodal segment with conspicuously warty surface. Basis of right fifth leg reaching about middle of first exopodal segment of left leg. Both endopod and exopod of right leg tapering into a spiniform process, each with a large tooth-like process proximally at about the same level.

Occurrence: A total of 238 specimens was found, which represented 4.2% of all *Euchirella* specimens found in the study. The species was found throughout the Gulf of Mexico and in all depth ranges sampled except the upper 100 m. No

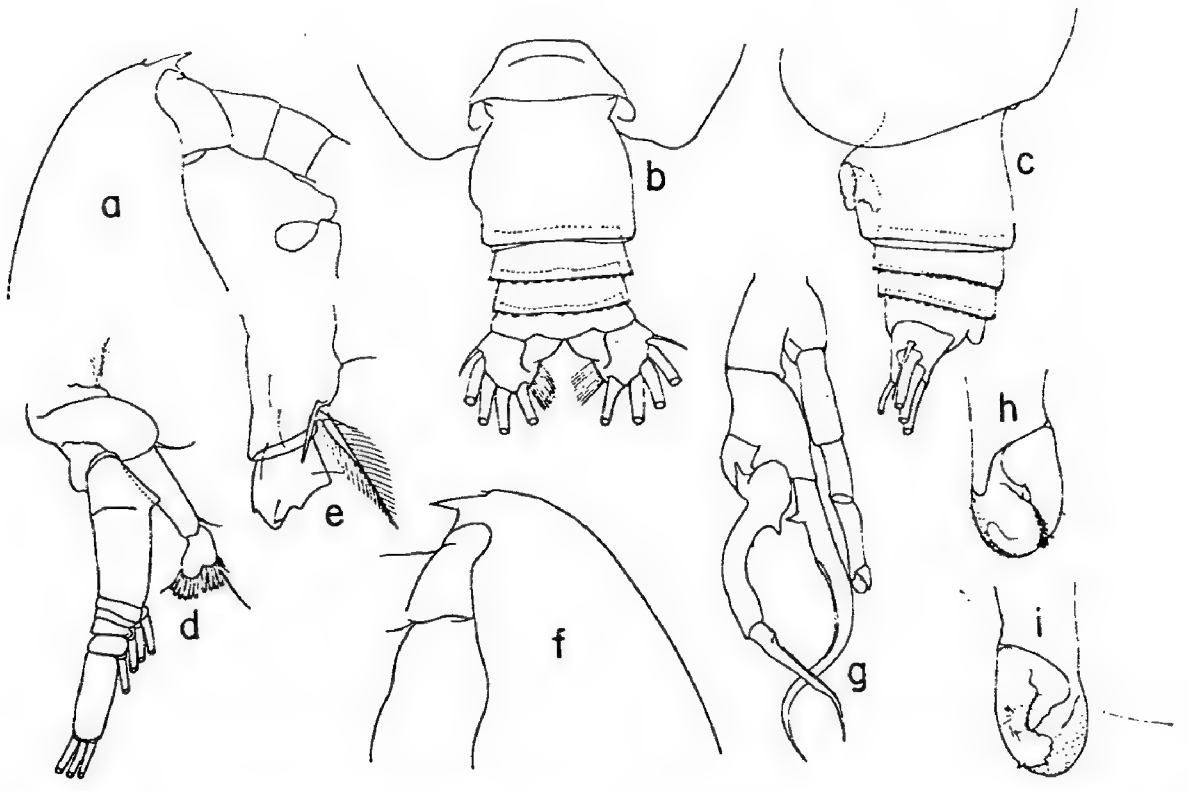


FIG. 6. *Euchirella pseudotruncata*. Female: a. forehead, lateral; b. posterior part of body, dorsal; c. *item*, lateral; d. antenna; e. coxa of fourth leg, posterior. Male: f. forehead, lateral; g. fifth pair of legs, anterior; h. distal part of left fifth leg, anterior; i. *item*, posterior.

significant difference in its vertical distribution was found between the day and night.

EUCHIRELLA PULCHRA (LUBBOCK, 1856) (Fig. 7)

This species was originally described by Lubbock (1856) under the name *Undina pulchra* from a male specimen obtained in the tropical Atlantic and has been fully redescribed including the female by Giesbrecht (1892) and again by Sars (1925). The species has been known to have a wide range of distribution over the tropical, subtropical, and temperate regions of the world oceans (Vervoort 1963). Recently, however, a northeastern Pacific population that had been considered as belonging to this species was recognized as a separate species (Park 1976). In the Gulf of Mexico, it has been recorded from the Florida Current (Owre 1962) and the western part of the Gulf (Park 1970).

Female: Body length based on 300 randomly selected specimens, 3.04–3.92 mm. Prosome length, 2.44–3.08 mm. Forehead devoid of a crest (Fig. 7a, b). Rostrum well developed. Posterolateral corners of metasome symmetrical, broadly rounded when viewed laterally (Fig. 7d). Dorsally, genital segment asymmetrical, with a large ear-shaped protuberance on left side (Fig. 7c). Endopod of antenna about 1/3.5 length of exopod (Fig. 7f). Inner and outer lobe of second endopodal segment each with 6 setae. Maxillule with 3 setae on basis, 4 on endopod, 11 on exopod, and 6 on outer lobe. Coxa of fourth leg with 2 large spines at base of inner seta (Fig. 7g).

Male: Body and prosome lengths based on 60 randomly selected specimens, 3.00–3.16 and 2.24–2.60 mm, respectively. Forehead with a low crest (Fig. 7h, i).

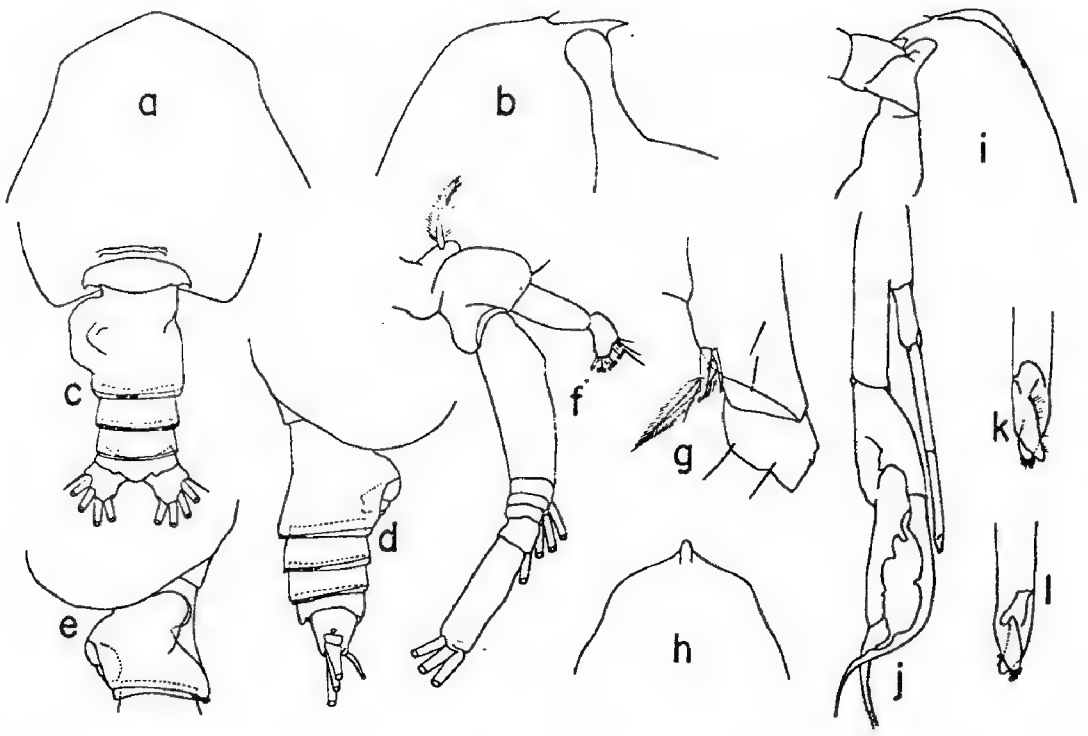


FIG. 7. *Euchirella pulchra*. Female: a. forehead, dorsal; b. *item*, lateral; c. posterior part of body, dorsal; d. *item*, right side; e. genital segment, left side; f. antenna; g. coxa of fourth leg, posterior. Male: h. forehead, dorsal; i. *item*, lateral; j. fifth pair of legs, anterior; k. distal part of left fifth leg, posterior; l. *item*, anterior.

Rostrum well developed. Left fifth leg without endopod (Fig. 7j). First exopodal segment far short of reaching distal end of right basipod. Third exopodal segment small, together with a similarly small distal process of second, forming a small chela (Fig. 7k, l). Both endopod and exopod of right leg tapering into a large spiniform process. Endopod with 4 processes along external margin, 2 proximal and 2 distal to joint between 2 exopodal segments. Anteriorly, 3 processes are visible on first exopodal segment, with first process hidden behind proximal part of endopod (Fig. 7j); 2 of these 3 processes are between first 2 processes of endopod.

Occurrence: *E. pulchra* was the most abundant species of the genus in the present study. Altogether, 2729 specimens were found; that is, 48.5% of all *Euchirella* specimens found in the study belonged to this species. During the daytime, the species was found in a depth range of 500–2000 m, with a high concentration between 500 and 1000 m. In the night, however, the species was also found in large numbers in the upper 200 m.

EUCHIRELLA ROSTRATA (CLAUS, 1866) (Fig. 8)

This species was originally described under the name *Undina rostrata* by Claus (1866) from female specimens obtained in the western Mediterranean Sea. Giesbrecht (1892) redescribed the species from the same area. The male was first described by Cleve (1900) and redescribed by Sars (1925). The species has been recorded widely over the tropical, subtropical and temperate regions of the world oceans (Vervoort 1957, Tanaka and Omori 1969a). In the Gulf of Mexico, it has been recorded from the Florida Current (Owre 1962) and the western part of the Gulf (Park 1970).

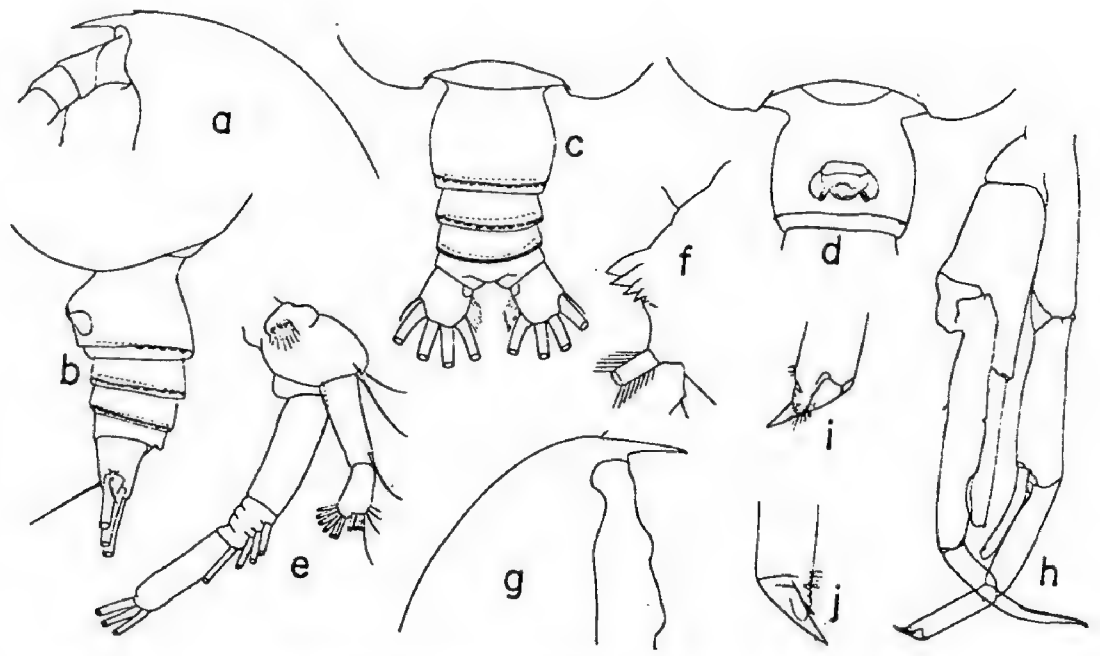


FIG. 8. *Euchirella rostrata*. Female: a. forehead, lateral; b. posterior part of body, lateral; c. *item*, dorsal; d. genital segment, ventral; e. antenna; f. medial side of coxa of fourth leg, posterior. Male: g. forehead, lateral; h. fifth pair of legs, anterior; i. distal part of exopod of left fifth leg, anterior; j. *item*, posterior.

Female: Body length based on 30 randomly selected specimens, 2.96–3.22 mm. Prosome length, 2.48–2.66 mm. Forehead without a crest (Fig. 8a). Rostrum large. Posterolateral corners of metasome symmetrically rounded either dorsally or laterally (Fig. 8b, c). Dorsally, genital segment symmetrical, with broadly swollen lateral sides. Endopod of antenna well developed, almost ½ length of exopod (Fig. 3e). Second endopodal segment with 8 setae on inner and 6 on outer lobe. Maxillule with 3, 3, 11 and 9 setae, respectively, on basis, endopod, exopod, and outer lobe. Coxa of fourth leg with a row of spines, gradually diminishing in size from proximal to distal (Fig. 8f).

Male: Body and prosome lengths of 2 specimens found in the study, 2.60 and 2.12 mm, respectively. Forehead without a crest (Fig. 8g). Rostrum larger than in female. In fifth pair of legs (Fig. 8h), left basipod much longer than right. Endopod on left leg well developed, reaching close to distal end of first exopodal segment. Third exopodal segment of a small conical form, together with a similar but smaller process of second, forming a chela (Fig. 8i, j). Right leg with club-shaped endopod reaching close to distal end of first exopodal segment. Second exopodal segment tapering into a spiniform process.

Occurrence: A total of 119 specimens was found in the study; that is, only 2.1% of all *Euchirella* specimens found in the study belonged to this species. Most of them were found in the eastern Gulf close to the Yucatan Channel and Straits of Florida. Its bathymetrical distribution ranged from a depth of about 200 m down to about 1000 m.

EUCHIRELLA SPLENDENS VERVOORT, 1973 (Fig. 9)

E. splendens was originally described by Vervoort (1963) from female specimens obtained in the Gulf of Guinea. Grice (1969) reported both the female and the male of this species from the Gulf of Mexico, but his male has subsequently been identified with *E. pseudotruncata* and its correct male has been discovered by Park (1975).

Female: Eighty randomly selected specimens measured 3.88–4.83 mm in body length and 3.28–4.04 mm in prosome length. No crest on forehead (Fig. 9a). Rostrum relatively small. Posterolateral corners of metasome symmetrically rounded. Dorsally, genital segment asymmetrical with a large protuberance distally on right side (Fig. 9b, c). Tip of protuberance often divided into 2 processes. Endopod of antenna about ¼ length of exopod (Fig. 9e). Second endopodal segment with 4 setae on inner and 5 on outer lobe. Maxillule with 3 setae on basis, 4 on endopod, 11 on exopod, and 8 on outer lobe. Coxa of fourth leg with 2 large spines at base of inner seta (Fig. 9f).

Male: Body and prosome lengths based on 22 specimens, 3.40–3.76 and 2.72–3.04 mm, respectively. Forehead devoid of a crest (Fig. 9g). Rostrum much better developed than in female. In fifth pair of legs (Fig. 9h), left basipod small, reaching only to distal end of coxa of right basipod. Endopod of left leg represented by a minute process. First exopodal segment reaching distal end of right basipod. Third exopodal segment small, together with a somewhat larger distal

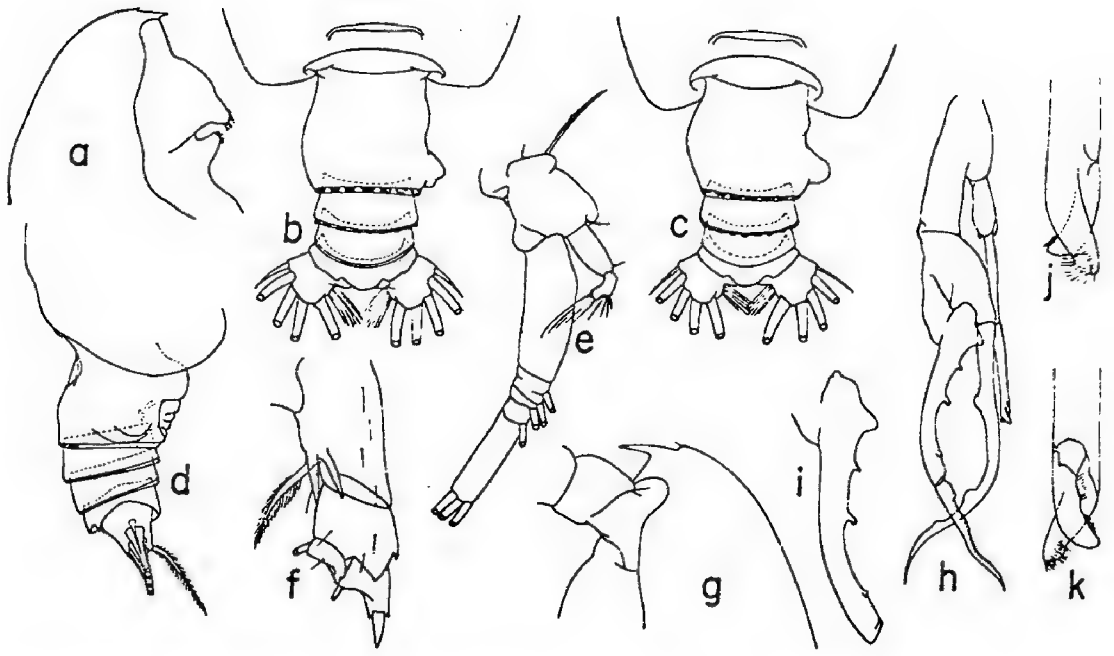


FIG. 9. *Euchirella splendens*. Female. a. forehead, lateral; b–c. posterior part of body of two different specimens, dorsal; d. *item*, lateral; e. antenna; f. basipod of fourth leg, posterior. Male: g. forehead, lateral; h. fifth pair of legs, anterior; i. first exopodal segment of right fifth leg, anterior; j. distal part of left fifth leg, anterior; k. *item*, posterior.

process of second, forming a chela (Fig. 9j, k). Both endopod and exopod of right leg tapering into a large spiniform process. First process of endopod about at same level as third process of first exopodal segment; second process located distal to joint between 2 exopodal segments.

Occurrence: *E. splendens* was the third most abundant species of the genus in this study. Altogether, 599 specimens were found, which represented 10.7% of all *Euchirella* specimens found in the study. The species was found throughout the Gulf of Mexico and its bathymetrical distribution during the daytime extended from a depth of about 200 m down to the deepest depth sampled (3000 m). In the night the species appeared in large numbers in the upper 100 m apparently as the result of an extensive vertical migration.

GENERAL REMARKS

The genus *Euchirella* is comprised of medium to large-sized marine planktonic copepods which are known to be mainly carnivorous (Mullin 1967). Characteristically, the females have strong mandibular blades and powerful spiniform setae on the maxillule, maxilla, and maxilliped that are primarily used in feeding. These mouthpart appendages show little variation among the species, which apparently suggests that their feeding methods are basically similar. The species, however, show various degrees of development in the endopods of the antennae, from the poorest condition found in *E. amoena*, in which it is only 1/5 the length of the exopod, to the best developed state found in *E. rostrata*, whose antennal endopod is almost as long as ½ the length of the exopod. The biological implication of this variability is not clear except for a possible phylogenetic significance. Otherwise, all the species are morphologically rather homogenous as far

TABLE 2

Average number of specimens taken per one-hour tow from various depths*

Day or Night	Day													Night					
Sampling Depths (m)	25	50	100	200	500	1000	2000	3000	200–0	200–100	500–200	1000–500	2000–1000	100–0	200–0	500	1000	2000	2000–1000
No. of Tows	4	5	4	9	4	4	3	1	2	1	2	2	3	3	2	3	1	1	1
E. amoena	2.0	6.2	1.8	0.2	0.1	0.5	0.5	—	6.5	8.0	—	1.0	2.1	4.8	3.0	0.2	—	—	2.0
E. bitumida	—	—	—	—	—	0.5	—	—	—	—	—	0.3	0.2	4.5	—	0.3	—	—	0.6
E. curticauda	—	—	—	—	0.1	3.4	0.3	0.3	—	—	—	4.4	1.3	12.7	16.4	0.3	0.5	1.0	1.4
E. maxima	—	—	—	—	0.3	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—
E. messinensis	—	—	—	—	3.0	16.9	—	—	—	—	8.9	12.0	1.7	26.7	15.4	0.3	1.5	—	1.7
E. pseudotruncata	—	—	—	6.8	0.3	0.3	0.2	0.3	7.7	1.0	3.9	0.3	0.3	—	1.4	—	—	0.3	0.3
E. pulchra	—	—	—	—	26.8	25.0	0.3	—	—	—	—	20.9	15.6	14.6	45.0	0.7	24.0	—	3.7
E. rostrata	—	—	—	0.2	—	—	—	—	1.0	1.0	—	4.5	—	—	—	0.2	—	—	—
E. splendens	—	—	—	5.6	1.3	4.1	1.2	1.0	6.7	34.0	5.0	2.9	4.6	6.7	10.0	0.2	1.5	3.7	1.1

* Two of the three night tows from 100–0 m and one of the two day tows from 200–0 m were taken with a one-meter net having a mouth area of about 0.78 m^2. All other tows were taken with paired Bongo nets that had a combined mouth area of about 0.77 m^2, and the two samples from each tow were combined. The towing speed was about 2.5 knots.

as the adult females are concerned, and they are distinguished mainly by the shape of the genital segment, presence or absence of a crest on the forehead, and number of spines on the coxa of the fourth leg.

As in the other genera of the family Aetideidae, the adult males have mouthpart appendages that are greatly reduced, particularly those parts of the appendages directly involved in feeding, such as the mandibular blades, gnathobases of the maxillule, and entire maxilla.

The males are mainly identified by comparing the anatomical details of the fifth pair of legs as in most of the other copepod species. According to the male fifth pair of legs, the *Euchirella* species found in the present study can be divided into 2 groups. 1). The group comprising *E. curticauda*, *E. maxima*, and *E. rostrata*, in which the left basipod of the fifth pair of legs is considerably longer than the right; the left leg has a well-developed endopod; the endopod of the right leg is club-shaped and much shorter than the exopod. 2). The group including *E. amoena*, *E. bitumida*, *E. messinensis*, *E. pulchra*, *E. pseudotruncata*, and *E. splendens*, in which the basipod of the left fifth leg is much shorter than that of the right; the endopod of the left fifth leg is entirely missing or represented by a minute process; the endopod of the right fifth leg is spiniform and about as long as the exopod.

In the present study none of the *Euchirella* species showed a restricted regional distribution. Except for the rarest species (*Euchirella maxima*), they occurred regularly throughout the Gulf of Mexico. Although the copepods were generally more abundant at stations close to the continental shelf, particularly to the Campeche Bank, the relative abundance of each species remained about the same at most of the stations (Table 1). The most abundant species was *E. pulchra*, which comprised 48.5% of all *Euchirella* specimens obtained; that is, this species was roughly equal in abundance to all the remaining species combined. The next 3 most abundant species (*E. messinensis*, *E. splendens*, and *E. curticauda*) together were represented by 37.3% and the remaining 5 species by only 14.2% of all the *Euchirella* specimens found in the study (5622).

As shown in Table 2, all the species exhibited a wide range of vertical distribution. Except for *E. amoena*, which was found from a depth of as shallow as 25 m, all the species were obtained only from depths exceeding 200 m by day, but in the night, practically all of them were caught in large numbers in the upper 100 m. These findings could be taken as evidences of their extensive diurnal vertical migration.

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TIDAL AND DIURNAL RHYTHMS OF LOCOMOTORY ACTIVITY AND OXYGEN CONSUMPTION IN THE PINK SHRIMP, *PENAEUS DUORARUM*

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ABSTRACT

Evidence for in-phase tidal and diurnal rhythms of activity, and oxygen consumption in the pink shrimp, *Penaeus duorarum*, was obtained by 24-hr experiments with oxygen monitoring and activity recording devices. Nocturnal activity was more pronounced than the daytime activity, even if high tide occurred in the daytime. Juveniles would start swimming at nightfall, even if it were the time of ebb tide in nature, and continue the activity until dawn hours. Some activity was observed in phase with daytime high tides. Tidal and diurnal rhythms were found to be superimposed on each other. After seven days in captivity the tidal rhythm decayed, while the nocturnal activity persisted.

Though oxygen consumption patterns generally followed activity cycles, metabolic rate might increase prior to the onset of intense locomotory activity. Also, oxygen consumption would reach a certain maximum, and would not increase further even if the swimming was more pronounced. An endogenous controlling mechanism for locomotory and oxygen consumption patterns is suggested.

That several marine organisms adapt their physiological processes to the phases of environmental tidal cycles is well known. Locomotory activity, oxygen consumption, and color changes are some of the functions that exhibit in-phase tidal rhythms. Apart from periodicities of tidal frequency, organisms also display circadian rhythms of biological functions. The reviews of Webb and Brown (1959), Cloudsley-Thompson (1961), Enright (1963), Harker (1964), Aschoff (1965), Bünning (1967), Brown, Hastings and Palmer (1970), Bennett (1974) and Palmer (1974) summarize our knowledge on biological rhythms.

Several species of penaeid shrimp perform extensive inshore and offshore migrations during their life cycle. Adults spawn in depths up to 100 m (Subrahmanyam 1971), and the postlarvae migrate into coastal low saline environments, which are subjected to tidal influences. In such habitats postlarvae and juveniles have been reported to be very active at night (Farfante 1969). During the course of routine investigation of oxygen requirements of juvenile pink shrimp, *Penaeus duorarum*, it became evident that captive shrimp showed higher activity and oxygen consumption at night, and also at the time of flood tides in nature. There is strong evidence that *P. duorarum* exhibits persistent activity rhythms related to tidal phases, lunar phases, and diurnal cycles of light (Fuss

1964; Fuss and Ogren 1966; Wickham 1967; and Hughes 1969a, 1969b, 1972). However, there is no information on the oxygen consumption patterns of this species as related to tidal rhythms of locomotory activity. This report presents quantitative data on tidal and diurnal activity and oxygen uptake cycles of pink shrimp, and also evidence for decay of tidal rhythms in captivity.

MATERIALS AND METHODS

Juveniles of pink shrimp were collected from turtle grass beds in 90 to 120 cm deep water close to the shore at low tides with a 9-m long seine. They were transferred to laboratory aquaria within three hours, and held at 20‰ salinity, and 25 ± 1 C temperature for 24 hours prior to the experiments. They were not fed during this time. The ambient salinity and temperature varied between 20 and 25‰, and 25 and 28 C respectively during the period of research. Experiments were conducted at the same levels of salinity and temperature, and within four days after the capture of shrimp. A new batch was collected for the next series. Filtered sea water was used for all the experiments. Single shrimps in the size range of 0.4 (42 mm) to 11 g (112 mm) were used in the experiments, and as many sizes as possible were tested. Only one experiment was run for each size. Group experiments were conducted with two shrimps in the chamber to test the group behavior.

In the experimental set-up, the respiration chamber with shrimp (RC), and a control chamber (C) were immersed in a 90–l Instant Ocean constant temperature tank (Fig. 1). The control chamber served to detect any changes in oxygen levels that were not due to shrimp respiration. The chambers had a capacity of 500 ml, and only one shrimp was used for individual experiments. For group experiments, only two small shrimp of same length and weight were used, since the chambers were not considered to be large enough to accommodate more subjects. Both the chambers were fitted with oxygen electrodes (OP), which were connected to YSI oxygen meters (OM_1 and OM_2), which were in turn connected to pen recorders (R_1 and R_2). The initial oxygen content was read, and the two recorders were calibrated at 100% for this concentration. Initial

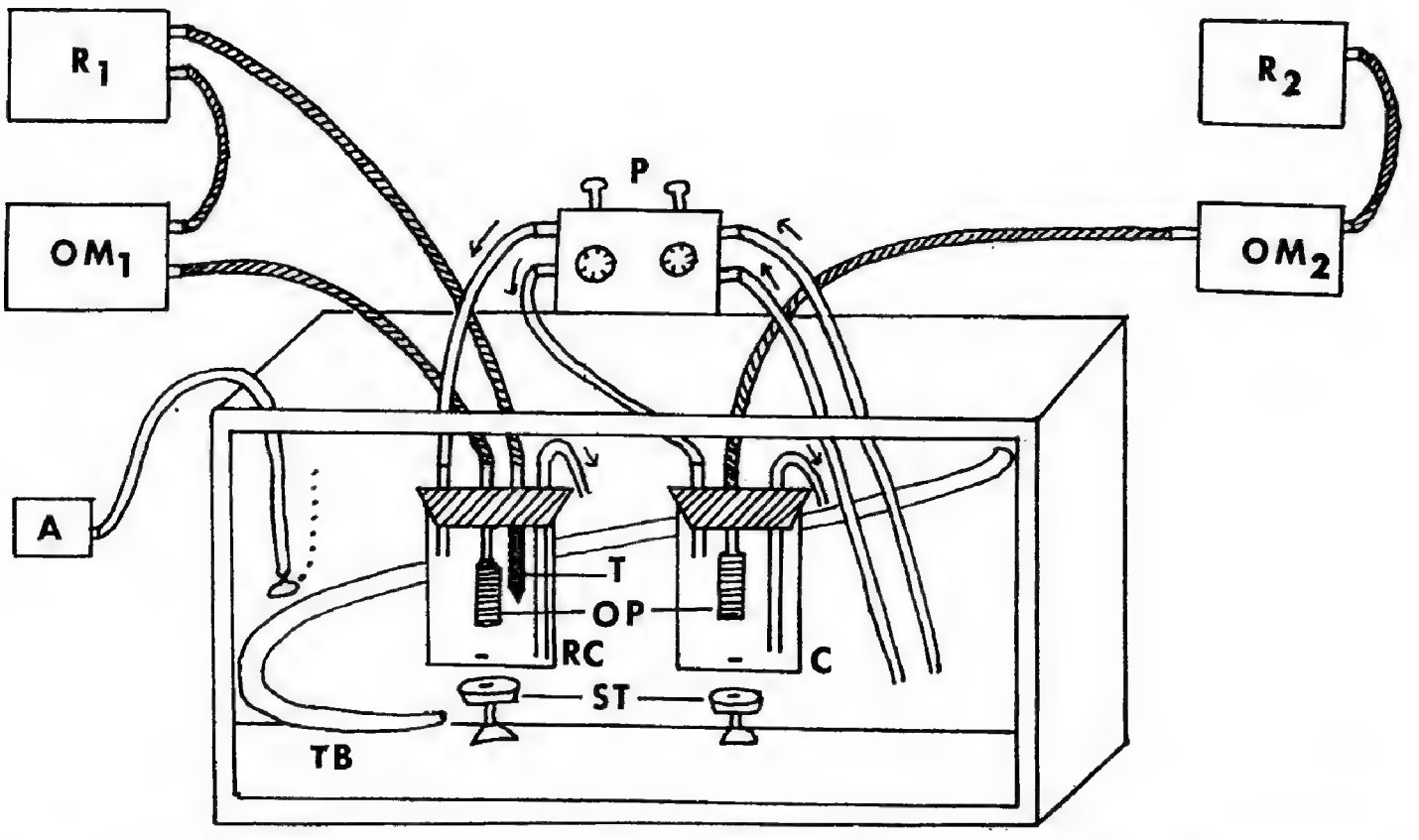

FIG. 1. The experimental set-up with continuous flow, and long-term recording of locomotory activity, and oxygen consumption (explanation given in text).

oxygen content was also determined by the Winkler method to check the accuracy of the oxygen meter. Oxygen consumption was derived from the drop in percentage on the recording (R_1). Winkler determinations were made once every six hours on the water samples drawn from RC to check the accuracy of oxygen meters. Initial oxygen content was maintained at 4.7 to 5.8 ml/l in the tank by constant aeration with an air pump (A). Oxygen content in the in-going water was constantly monitored on OM_2 and R_2. The oxygen probes were activated by small 10 mm stirrers turned by magnets set in rubber stoppers (ST), which were in turn rotated by flow of water through a tube (TB). The rotation of stirrer did not prevent shrimp from being quiescent because the stirring was not strong enough to disturb the shrimp, though sand was not provided in the respiration chamber. The oxygen probe in the control chamber normally registered no changes from the initial oxygen content. Appropriate corrections were applied to the data for the flow of water. A metered pump (P) delivered 1000 to 1200 ml of water per hour into the chambers. If any changes were detected in the oxygen levels in the control chamber appropriate corrections were applied to the oxygen consumption data.

Activity recordings were made with a thermistor device (T) connected to R_1. This was built locally according to the design of Heusner and Enright (1966). In principle, two thermistors, one outside and one inside of the chamber, were used. A 90-volt DC current was fed into the thermistors. Voltage variations across a Wheatstone bridge were related to the movements of water caused by the swimming activity of the shrimp. These movements were recorded as pen strokes on the recorder. The number of strokes per hour represented the intensity of activity.

The entire set-up was placed under overhead lights, and the lights were turned off and on simulating natural diel periods of light and darkness of the season. Each experiment was run for at least 24 hours, and in some cases for 36 hours.

RESULTS

Tidal Rhythm

The amplitudes of semidiurnal tides, and activity and oxygen uptake patterns of various sizes of juvenile pink shrimp are illustrated in Figures 2 and 3. The 0.44 g, 0.52 g, 1.68 g, and 3.65 g shrimp (Fig. 2), and the 9.66 g and 11.0 g shrimp (Fig. 3) exhibited higher activity during the phases of natural flood tides. The nocturnal tidal activity was more pronounced compared to the daytime, even if the amplitudes of tides did not vary significantly. The 11.0 g shrimp, however, was slightly active during most of the day, but showed elevated activity during high tide phase (Fig. 3F). Similar trends of locomotor activity were observed in the paired shrimp experiments (Fig. 3G, H).

As one would expect, oxygen consumption increased during high tide phase in approximate synchrony with activity. In some cases, rise in oxygen uptake occurred an hour prior to the increase in activity (arrows in Fig. 2D, and Fig. 3G H). Oxygen uptake by shrimp doubled in almost all cases during the active phase. In several cases, however, oxygen consumption registered an initial increase, and reached a plateau without further rise, corresponding to higher swimming activity occurring an hour or two later (Fig. 2A, B, D). This point is further illustrated with the data presented in Table 1. It is seen that all sizes of shrimp consumed more oxygen during the periods of pronounced swimming, but did not consume more in response to further rise in activity. It appears that pink shrimp reaches a plateau of oxygen uptake during the active phase at a certain level of activity. Oxygen consumption patterns of paired shrimp were also in

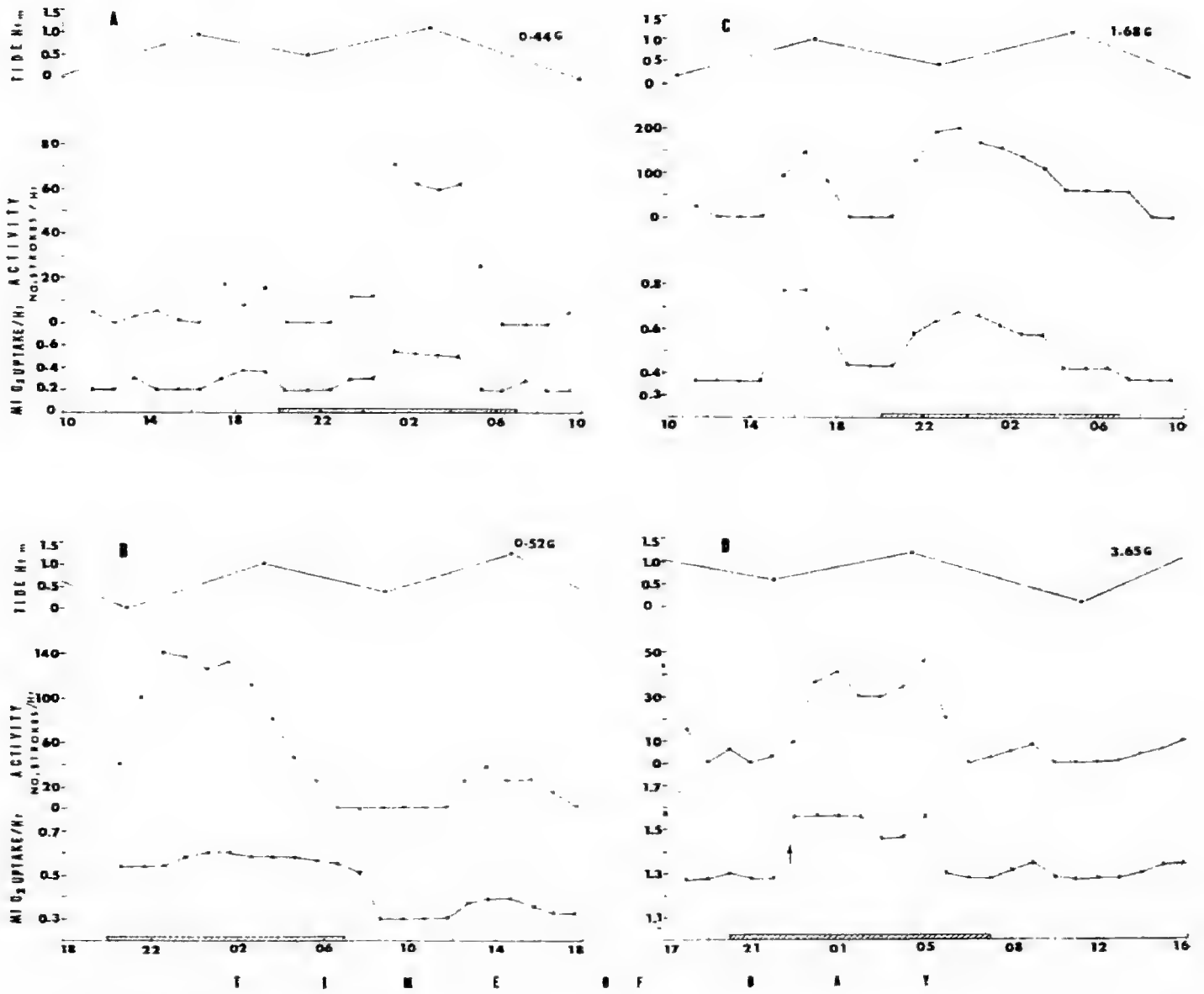

FIG. 2. The tidal amplitudes, and activity and oxygen uptake patterns of four juvenile pink shrimp. Slanted bars indicate night.

TABLE 1

Oxygen consumption rates (ml/hr) as related to activity (strokes/hr) in juvenile pink shrimp

Size	0.44 g		1.68 g		3.65 g		9.66 g		11.0 g	
	Activity	O_2 uptake	Activity	O_2 uptake	Activity	O_2 uptake	Activity	O_2 uptake	Activity	O_2 uptake
	0	0.20	0	0.34	0	1.30	0	1.30	0	2.20
	2	0.20	10	0.40	2	1.30	21	1.30	4	2.30
	5	0.20	15	0.40	5	1.30	25	1.30	10	2.30
	12	0.30	20	0.40	16	1.56	32	1.30	14	2.43
	16	0.30	110	0.60	20	1.56	40	1.30	20	2.44
	18	0.30	120	0.60	26	1.56	50	1.30	32	2.44
	60	0.40	130	0.60	30	1.56	66	1.80	36	2.50
	63	0.40	145	0.60	36	1.56	72	1.90	40	2.50
	76	0.40	195	0.60	42	1.56	82	1.90	42	2.50
	85	0.40	210	0.60	45	1.60	92	1.90	45	2.50

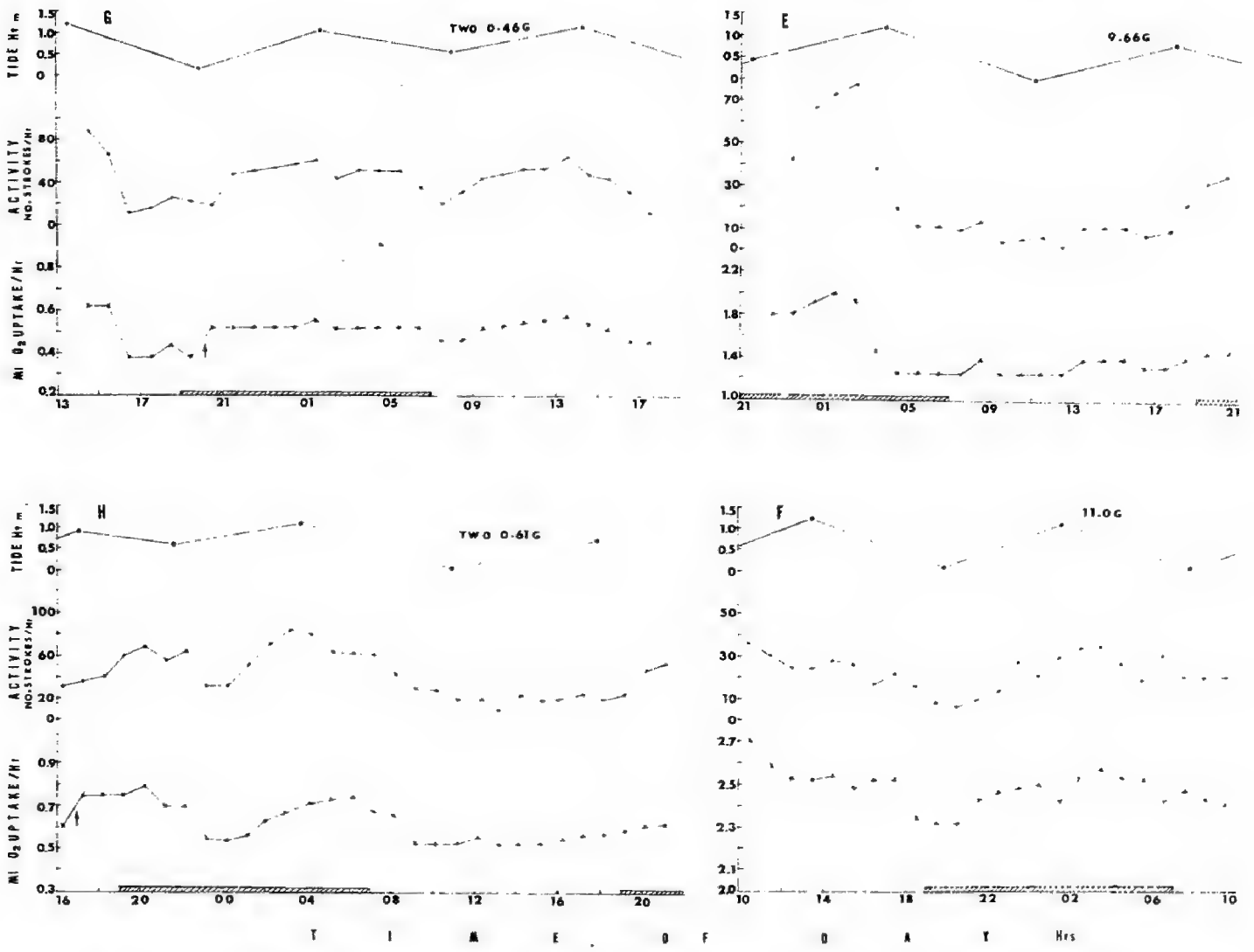

FIG. 3. The tidal amplitudes, and activity and oxygen uptake patterns of two juvenile pink shrimp (E and F), and two shrimp grouped together (G and H). Slanted bars indicate night.

approximate synchrony to activity, and there is an indication of plateau of oxygen uptake (Fig. 3G, H).

Diurnal Rhythm

In the holding tanks, shrimp would lie quiescently buried in sand during daytime, with only the eye stalks visible over sand. They would emerge at certain times of day, and at night, and swim actively. In the experimental chambers shrimp would lie on the bottom quietly in spite of the stirring of water by the stirrer. The recordings show that shrimp were active at night, and consumed more oxygen correspondingly (Figs. 2 and 3). If the high tide occurred at night, activity and oxygen uptake were more pronounced than during daytime high tide phase (Fig. 2A, B, C, and Fig. 3E, F). In these instances the amplitude of nocturnal tides was not significantly higher than the daytime high tides. In some cases, activity increased by nightfall, even if the tide was at ebb in nature, and reached a peak at subsequent high tide (Fig. 2B, D, and Fig. 3E). Also, activity continued into dawn hours, even after the ebb tide (Fig. 2C, D, and Fig. 3F). Oxygen uptake followed similar patterns. In the paired shrimp experiments, both individuals were active and quiescent synchronously indicating certain cohesion of aggregation. The intensity of activity of paired shrimp was not greater than

that of individual shrimp. It was as if there was only one shrimp in the experimental chamber. Higher nocturnal activity, onset of increased activity in the evening, and continuous high activity until dawn hours with corresponding oxygen uptake trends were observed for the paired shrimp.

Waning of Tidal Rhythm

Some juvenile shrimp, which were held in captivity for more than a week, were observed to be quiescent throughout the day. They would emerge from the sand only when lights were turned off in the evening. Two such shrimp were tested in the last series, in order to find out whether their tidal rhythms were

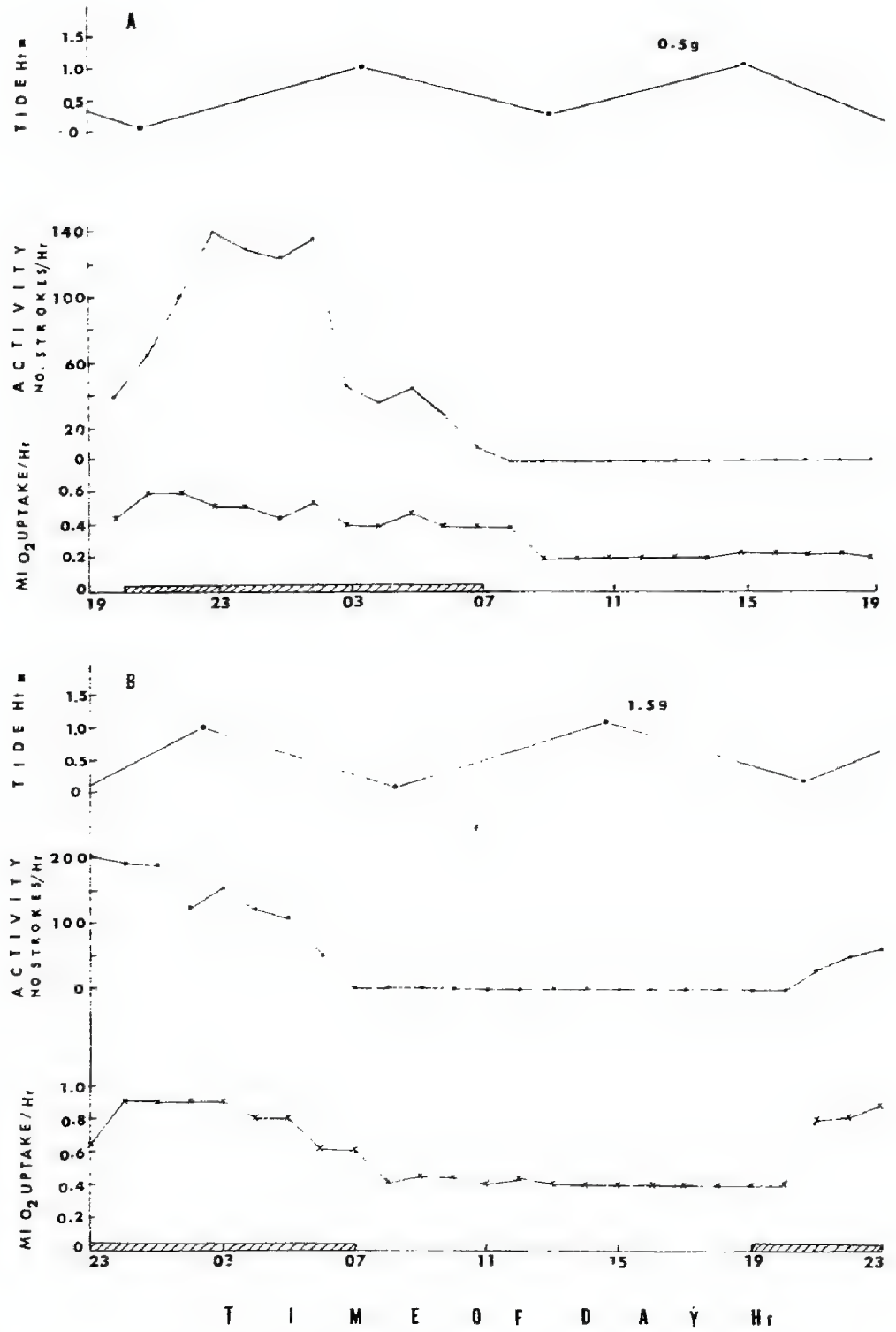

FIG. 4. The tidal amplitudes, and activity and oxygen uptake patterns of two juvenile pink shrimp held captive for more than seven days. Slanted bars indicate night.

persistent for long periods of time out of their natural habitat. The recordings for 0.5 g and 1.5 g shrimp in Fig. 4 show that the tidal phase of activity and oxygen consumption had decayed, and only nocturnal activity persisted. This suggests a waning of tidal rhythm after seven days in the absence of entrainment by environmental tides.

DISCUSSION

This report presents quantitative evidence for locomotor activity patterns of *P. duorarum* related to tidal cycles and to diurnal light cycles. Shrimp were most active at nights during high tide phase, and less active during daytime high tide period. They also exhibited enhanced swimming even during ebb tide phase at night, indicating the presence of a distinct and independent nocturnal activity phase unrelated to tides. It is evident that the two rhythms are superimposed on each other. Though tidal rhythms persist for less than a week and then wane, nocturnal activity is more persistent. Oxygen consumption shows synchronous increase with higher activity. However, two significant points of this investigation are that oxygen consumption may rise even before the start of intense activity, and it may reach a certain plateau beyond which it does not increase regardless of more pronounced subsequent swimming movements. These two aspects of metabolism in pink shrimp have not been reported earlier.

Several littoral decapods synchronize their activity patterns to the environmental tidal phases, or diurnal light cycles, or to both. Some species show higher activity during high tide phases, such as *Uca* (Brown *et al.* 1956, Bennett *et al.* 1957, and Palmer 1973), *Carcinus* (Naylor 1958), *Sesarma* (Palmer 1967), *Emerita asiatica* (Chandrashekaran 1965), *Palemon species* (Rodriguez and Naylor 1972) and *Penaeus duorarum* (Wickham 1967; and Hughes 1969a, 1969b, and 1972). Diurnal rhythmicity superimposed on tidal patterns have been reported for color changes in *Uca* (Brown *et al.* 1953), locomotor activity in *Callinectes sapidus* (Fingerman 1955), *Carcinus maenas* (Naylor 1958) and *P. duorarum* (Wickham 1967, and Hughes 1969b). Oxygen consumption are normally related to in-phase tidal activity as in *Uca* (Brown *et al.* 1954), *E. asiatica* (Chandrashekaran 1965) and *P. duorarum* (present study). The question, then, is which component, either tidal or diurnal, is completely endogenous, and which is entrained by external stimuli. Also, which activity pattern is more important for the survival of a migratory species such as the pink shrimp.

Penaeus duorarum in the present study exhibited more pronounced nocturnal activity especially if high tide occurred at night. It was active even during ebb tide phases at night. After a week the tidal component waned, but the nocturnal activity persisted, which indicates that the tidal activity would decay after a period of time if shrimp were removed from the natural habitat. Fuss and Ogren (1966) and Wickham (1967) have shown that higher nocturnal phase locomotory activity of *P. duorarum* persisted even under constant light and dark conditions. Wickham (1967) also reported that tidal rhythm was less persistent

in captivity. Hughes (1969b) reported that tide-related locomotory activity lasted only for three days. In view of these criteria it appears that diurnal activity of pink shrimp is endogenously controlled (*cf.* Palmer 1974), while the tidal rhythms require frequent entrainment by external cues. Tides may act as *Zeitgeber* for tidal rhythmicity. The present author's conclusions are in agreement with Wickham (1967) and Hughes (1969b). Active swimming at night, especially during high tide phase in the natural environment, would be of great survival value to the juveniles of pink shrimp in their offshore migratory movements from low saline habitats. This behavior appears to be innate even in very young shrimp. Since juveniles appear to synchronize their locomotory rhythms, as indicated by paired shrimp, they can maintain a cohesion of aggregation. This ability would facilitate mass migrations of juveniles to offshore environment.

Oxygen consumption is a function of metabolism, and one would expect synchronous increase in oxygen uptake in response to heightened activity and *vice versa*. *Uca* (Brown *et al.* 1954), *Emerita* (Chandrashekaran 1965) and *P. duorarum* (present study) show such oxygen consumption patterns. However, several pink shrimp did not consume more oxygen after reaching a maximum uptake rate regardless of subsequent intense swimming activity. It would appear, therefore, that some metabolic adaptation exists in this species, which cuts down oxygen demand during sustained periods of high activity. Probably this behavior is also endogenously controlled and needs further investigation. Another interesting aspect is that oxygen consumption increases even prior to the commencement of intense activity in some juveniles. Such behavior was also noticed in *Carcinus maenas* (Arudpragasam and Naylor 1964). An endogenous controlling mechanism for such metabolic patterns has been suggested by Aschoff (1965). Some penaeid species regulate their oxygen consumption in relation to ambient oxygen tension, consuming more if available (Subrahmanyam 1962). Therefore, a higher activity phase during high tides, which will demand more oxygen from the environment than during a quiescent phase, would be of significant survival value to penaeid shrimp.

ACKNOWLEDGMENTS

This investigation was carried out by the author at Florida State University, and supported by Armour and Company, and United Fruit Company under a Grant No. OPPE 83–872. I would like to thank Dr. C. H. Oppenheimer for support and encouragement, and Dr. William Brogden for helping to build the activity recording device and other courtesies.

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SEASONAL PATTERNS IN THE RESPIRATORY METABOLISM OF THE MULLETS *MUGIL CEPHALUS* AND *MUGIL CUREMA*

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ABSTRACT

Respiratory metabolism of striped mullet, *Mugil cephalus*, and white mullet, *Mugil curema*, was studied in relation to weight, temperature, and swimming speed. Both species exhibit a general pattern of seasonal acclimatization similar to that seen in other fish species. Likewise, regression coefficients relating oxygen consumption to the other variables were usually within published ranges, except for swimming speed coefficients for white mullet which were exceptionally high. These specific patterns of regression coefficients and metabolic rates are consistent and can be used to partially explain the differences in distribution and ecology observed between the two species of mullet. The seasonal distributions and abundances of the two species as well as their metabolic responses and temperature sensitivities all indicate that the white mullet is a more warm-adapted species than the antitropically distributed, eurythermal striped mullet.

INTRODUCTION

The purpose of this study was to investigate the respiratory metabolism of the striped mullet, *Mugil cephalus*, and the white mullet, *Mugil curema*, in relation to weight, temperature, swimming speed, and season and to relate differences in these responses to the ecology of the two species.

The striped mullet is one of the most abundant estuarine fishes in warm-temperate and subtropical waters around the world, while the white mullet is found primarily in the tropical Atlantic Ocean off the coasts of both North and South America and West Africa. In the northwestern Gulf of Mexico, off the coast of south Texas, both species occur. In this region, as well as off most of the southeastern United States, *M. cephalus* is a year round inhabitant occurring in a variety of marine and estuarine habitats with salinities between 0 and over 80 ppt (Breuer 1957, Moore 1974). The white mullet is found in these regions only during the warmer months, from April through October off south Texas, with only occasional strays showing up in the winter (Moore 1974). In addition, white mullet occupy a more restricted range of habitats; although some may occur in very low salinities or in hypersaline water, a majority of the white

mullet collected in south Texas are found in salinities between 20 and 35 ppt (Breuer 1957, Parker 1965, Moore 1974) and predominately in areas close to the passes linking the bays with the Gulf of Mexico (Gunter 1958, Moore 1974).

MATERIALS AND METHODS

Mullet were collected from the Gulf of Mexico and estuarine habitats near Port Aransas, Texas with cast nets and seines. Live fish were transported to the laboratory in insulated boxes containing aerated sea water from the collection site.

In the laboratory, fish were held in temperature-controlled aquaria containing water which initially approximated ambient temperature and salinity conditions (Table 1). The temperature was then gradually changed (no more than 0.5 C per hour and no more than 5.0 C per 24-hour period) to the predetermined experimental levels at which the fish were acclimated for two days. Respiratory experiments were conducted in each season at temperatures of 12, 14, 17, 22, and 28 C with additional experiments at 9 or 10 C in the winter and 30 C in the summer. During the entire acclimation period the fish were not fed; however, no ill effects were observed.

Although Sidell *et al.* (1973) have indicated that thermal acclimation at the enzymatic level may require considerably more time, previous experience with striped mullet (Wohlschlag and Moore, ms) and other species (Wohlschlag *et al.* 1968, Moore 1973a) indicate that two days acclimation is sufficient to produce consistent levels of oxygen consumption in swimming fish.

Salinity remained constant during any single experiment and varied no more than 8 ppt during any season. Over the entire year salinity varied between 23.1 and 36.0 ppt.

Respiratory metabolism determinations were conducted in closed plexiglas chambers rotated by an electric motor. Two chambers of 10,450 and 42,190 ml and mean circumferences of 1 and 2 meters respectively were used to accommodate a range of fish sizes. The chambers and basic experimental design have been described by Wohlschlag (1964), Wohlschlag *et al.* (1968), and Moore (1973a). The basic outline of the procedure is as follows.

Single fish were introduced into the respirometer which was suspended in the aquarium in which the fish had been acclimated. It is our experience that this technique minimizes handling and the use of water conditioned by the presence of the fish reduces the time required for further acclimation to experimental conditions. Once swimming was induced by rotation of the chamber the speed of rotation was adjusted to match the swimming velocity which the fish most consistently maintained; usually steady swimming levels were achieved within 5 minutes after their introduction into the chamber. Thereafter the fish was allowed a 15-minute period of undisturbed swimming before the chamber was sealed and the oxygen consumption measurements begun. If steady swimming was not attained within 30 minutes the fish was discarded. Swimming was

TABLE 1

Summary of experimental seasonal variables

Species	Season	No. of fish tested	Average values and ranges		
			Weight (g)	Temp. (°C)	Swimming velocity (L/sec)
Mugil cephalus	Winter	31	143 (28–664)	19 (9.3–28.0)	0.95 (0.18–2.24)
	Spring	24	118 (24–685)	18 (10.8–27.7)	0.67 (0.03–2.80)
	Summer	18	172 (45–436)	19 (12.4–28.3)	0.69 (0.05–2.23)
	Fall	27	138 (15–628)	19 (9.7–28.6)	0.81 (0.01–2.60)
Mugil curema	Winter	10	99 (15–204)	18 (12.1–27.8)	1.20 (0.02–2.76)
	Spring	18	122 (19–230)	21 (12.7–28.2)	1.35 (0.01–3.85)
	Summer	24	140 (4–179)	24 (14.1–28.6)	0.65 (0.03–3.25)
	Fall	22	30 (10–253)	21 (13.9–28.1)	2.40 (0.89–3.19)

interrupted at 10-minute intervals for removal of a small water sample for dissolved oxygen analysis. At these times the aquarium temperature and the rotations of the chamber since the last sample period were noted. The addition of oxygen to the chamber by the replacement of the water sample with aquarium water was corrected for in the final calculation of oxygen consumption rates. Three such samples were usually taken, however if the fish appeared disturbed during any one period the sampling was continued until three consecutive "undisturbed" periods had passed. Minor changes in swimming velocity were compensated for by adjusting the rotation speed. Following each experiment the fish was weighed, measured, and sacrificed for sex and maturity determination. Scale samples were also taken at this time for subsequent growth analysis.

The careful observation of the fish's swimming and appropriate adjustments of the speed of rotation permitted the measurement of metabolic rates at swimming speeds determined mostly by the fish's preference and which will hereafter be referred to as *ad libitum* swimming speeds. The validity of the assumption that these are indeed preferred swimming speeds was tested by observing mullet swimming in nature. Migrating schools of fish were timed as they passed between two markers in the Aransas Pass Inlet. In addition, individual fish or smaller schools were observed swimming over measureable distances in local boat basins and marinas. The swimming speeds observed in these ways approximate those of the mullet in the respirometer, although the natural rates were much more variable. Aside from measurements at these *ad libitum* speeds the fish could usually be forced to swim at other predetermined velocities. This technique was only used to provide adequate ranges of swimming velocities for regression analysis and such values are not included in mean *ad libitum* swimming velocity calculations.

Dissolved oxygen levels in the chambers were measured by means of a Radiometer E5046 oxygen electrode and PHM71 gas analyzer. Oxygen consumption of the fish was related to weight, temperature, and swimming speed by multiple regression equations of the form:

$$\hat{Y} = a + b_w X_x + b_t X_t + b_v X_v$$

where:

$\hat{Y}$ is the expected value of oxygen consumption ($\log_{10}$ mg O_2/hr);
a is a constant, the y-interpret;
b_w, b_t, and b_v are multiple regression coefficients for weight, temperature, and swimming speed respectively; and
X_w, X_t, and X_v are weight ($\log_{10}$ gms), temperature (C), and swimming speed (lengths/sec, L/sec).

Regressions were computed on the University of Texas CDC 6400/6600 system using an inverse stepwise regression program.

RESULTS AND DISCUSSION

Averages and ranges of variables for both species over four seasons are in Table 1. Seasonal multiple regression equations for both species are given in Table 2. Statistics for these equations appear in Table 3, and seasonal averages for oxygen consumption (mg O_2/hr/kg for an average sized, 140 g, fish) for fish at different levels of activity, as calculated from the multiple regression equations are given in Table 4. Table 5 shows the results of statistical tests comparing seasonal multiple regression equations for both species.

The Effects of Weight on Metabolism

Most fish species have weight metabolism coefficients in the range of 0.67 to 1.00 (Winberg 1956). High weight coefficients were found in the present study for striped mullet during the spring and summer and for white mullet during

TABLE 2

Seasonal multiple regression equations for mullet respiration

Mugil cephalus, striped mullet
Winter, N = 31.
$$Y = -0.5705 + 0.7851\,X_w + 0.0247\,X_t + 0.0978\,X_v$$
Spring, N = 24.
$$Y = -1.8490 + 1.0471\,X_w + 0.0503\,X_t + 0.2471\,X_v$$
Summer, N = 18.
$$Y = -1.7483 + 1.0560\,X_w + 0.0417\,X_t + 0.1465\,X_v$$
Fall, N = 27.
$$Y = -0.7249 + 0.7839\,X_w + 0.0324\,X_t + 0.0327\,X_v$$

Mugil curema, white mullet
Winter, N = 10.
$$Y = -0.3942 + 0.8272\,X_w + 0.0024\,X_t + 0.1855\,X_v$$
Spring, N = 18.
$$Y = -0.6707 + 0.8348\,X_w + 0.0188\,X_t + 0.2015\,X_v$$
Summer, N = 24.
$$Y = -0.6920 + 0.6468\,X_w + 0.0295\,X_t + 0.2250\,X_v$$
Fall, N = 22.
$$Y = -2.2759 + 1.2495\,X_w + 0.0370\,X_t + 0.2916\,X_v$$

the fall (Table 2). These high values and the low weight coefficients seen in white mullet during the winter are all statistically different ($p<.01$) from Winberg's mean value of 0.85. These may be due to increased activity levels (Brett 1964; Beamish 1964a, 1970) or to a statistical interdependence between weight and swimming speed (Moore 1973b). Since the lowest weight coefficients for each species occurred in their respective spawning seasons, the observed seasonal differences in weight coefficients probably represent changes in the amount of tissues with low metabolic rates such as mature gonads or stored fats which are typical typical of actively spawning fishes.

TABLE 3

Regression statistics for seasonal mullet respiration equations

Equation	N	Multiple correlation coefficient R	Std. dev. of estimate S_y	Standard deviations of regression coefficient (S_b) and probabilities (P)					
				S_{b_w}	P	S_{b_t}	P	S_{b_v}	P
Winter, *M. cephalus*	31	0.87	0.1581	0.0873	**	0.0057	**	0.0464	**
Spring, *M. cephalus*	24	0.90	0.1894	0.0965	**	0.0080	**	0.0777	**
Summer, *M. cephalus*	18	0.93	0.1145	0.0954	**	0.0058	*	0.0524	*
Fall, *M. cephalus*	27	0.88	0.1504	0.0653	**	0.0049	**	0.0450	NS
Winter, *M. curema*	10	0.87	0.1499	0.1507	**	0.0101	NS	0.0596	**
Spring, *M. curema*	18	0.97	0.1647	0.0663	**	0.0089	*	0.0754	*
Summer, *M. curema*	24	0.92	0.1371	0.0787	**	0.0068	**	0.0346	**
Fall, *M. curema*	22	0.92	0.1641	0.1115	**	0.0080	**	0.0917	**

Probabilities: ** = highly significant, $P<0.01$; * significant, $0.01<P<0.05$; NS = not significant, $P>0.05$.

The Effect of Temperature on Metabolism

Although metabolic responses to small temperature ranges have often been expressed as linear regressions, recent unpublished data by Longley (1976) indicates that there may frequently be an important quadratic effect in temperature responses of the hermit crab, *Clibinarius vittatus*. To say whether this is also true of mullet or of fish in general would require considerable reevaluation of past and present data. Consequently I have utilized only a linear relationship between temperature and oxygen consumption to facilitate comparisons of my data with those of other authors.

Temperature coefficients for both species are generally within the range reported by others (Brett 1970, Fry 1971) except for the very small (not statistically different from zero) coefficient found for white mullet in winter. As this equation was based on only ten individuals captured during the winter months it is possible that the small sample size affected the results, although, aside from temperature, other responses were within expected limits. I have also shown (Moore 1974) that white mullet are generally absent from the south Texas coast during the winter so therefore these ten fish were somewhat unusual and may have experienced considerable temperature stress before capture. At temperatures of 12.5 C the white mullet generally became moribund, except in the winter when they remained active at 12.0 C. Although the fish in question were captured at 13–14 C, it is not improbable that they were under some stress from the low winter temperatures which could have depressed or altered their responses even to the higher experimental temperatures. Respiratory rates at 14 C were intermediate between spring and summer values, and at higher and lower temperatures there was no change from this 14 C-level (Figure 1). In this case acclimation times were probably insufficient to allow the stressed white mullet to readjust to both higher and lower temperature levels. Both seasonal abundance and low-temperature tolerance of the white mullet suggest a more warm-adapted physiology than occurs in the striped mullet which is present year-round and which tolerates temperatures down to 4 C (Moore 1974, 1976).

The Effect of Swimming Speed and Activity on Metabolism

Swimming speed coefficients obtained for white mullet were much higher than those obtained for striped mullet (Table 2) which approximated those commonly reported for other fish species (Winberg 1956, Wohlschlag 1962 Brett 1964, Brett and Sutherland 1965, Wohlschlag *et al.* 1968, Tytler 1969, Beamish 1970, Moore 1973a). Because of the physical similarity between the two species of mullet, morphological differences could not be responsible for the differences in swimming energetics. White mullet generally swam at higher relative velocities (which may be related to their smaller size) than striped mullet (Table 1). This discrepancy may be the cause of the observed differences in swimming coefficients, however a comparison of swimming coefficients between groups of large and small striped mullet indicate no similar size-specific differences. Therefore the higher coefficients may indicate that white mullet are less efficient in utilizing

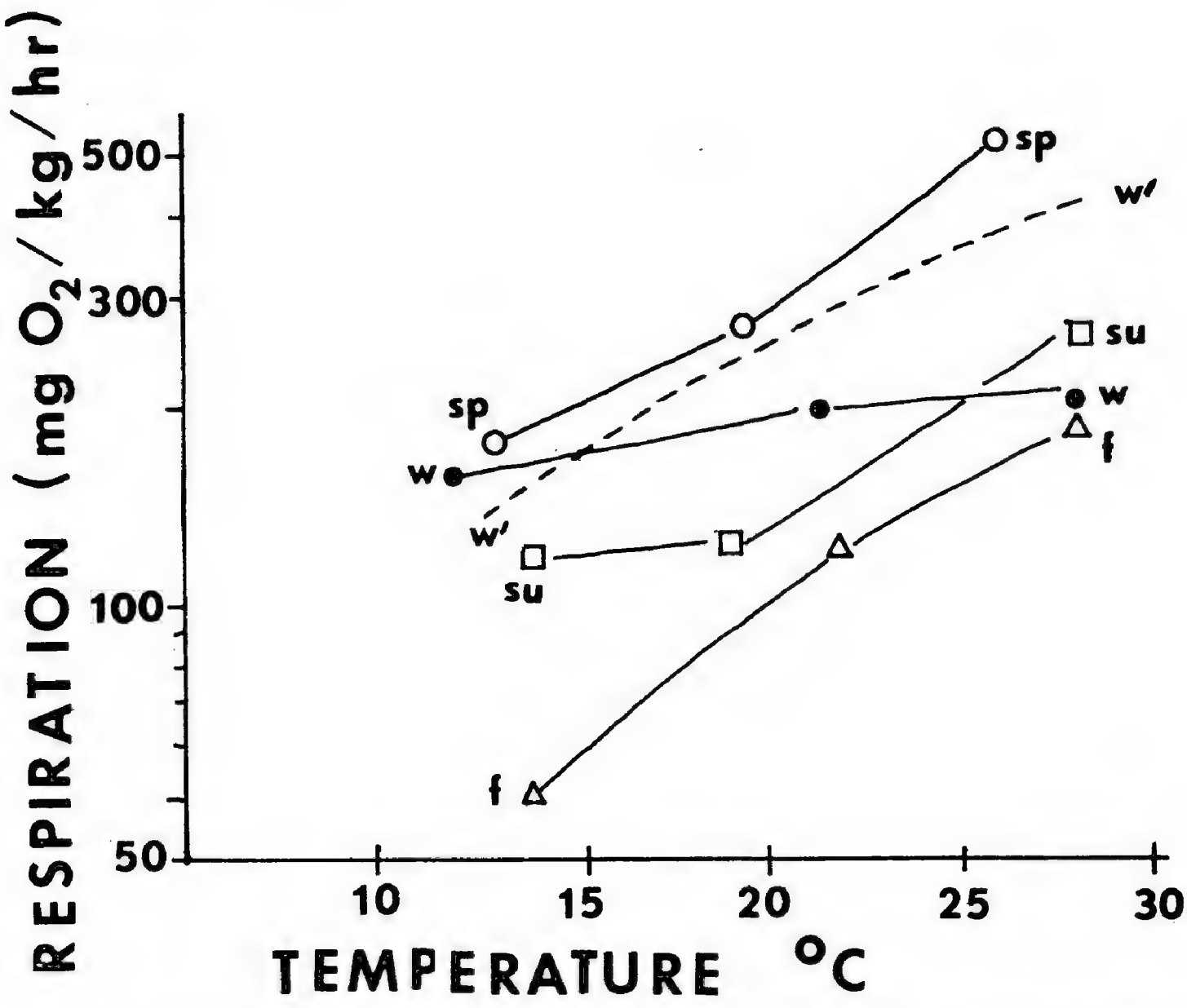

FIG. 1. Seasonal respiration for white mullet. Seasons abbreviated: w = winter, f = fall, sp = spring, su = summer. Dotted line (w') illustrates projected winter metabolism based on observed values at 14 C and $b_t = 0.03$.

energy for swimming than are striped mullet over the range of temperatures studied. Zimmerman (1965) has shown that the ecological energetics of a species should be considered as an adaptive mechanism. The apparent inefficiency of white mullet would then lead to the conclusion that this species is not as well adapted as the striped mullet to the environmental conditions of the south Texas area.

Physiological and Energetic Differences

Conservation or efficient utilization of energy plays an important role in the bioenergetics of a species and must be regarded along with other physiological and morphological adaptations in determining the fitness of a species. Since swimming is a necessary part of the life cycle of both mullets, the white mullet must be at an overall annual energetic disadvantage when compared to the striped mullet so that other aspects of the white mullet's energetics besides respiration should also be affected. Data on growth rates for both species of mullet (Moore

1973b) indicate the existence of two growth regimes among white mullet; one population of faster growing fish was collected only at the start and the close of the breeding season (i.e. only in the spring and again in the late summer) and a second population of slower growing fish was present for a greater part of the year. The growth rate of the fish in the former population exceeded that of the striped mullet, while that in the latter population was much lower. It is my belief that the fast-growing population represents migrant fish which spend most of the growing season either farther south or farther offshore while the slow-growing population represents those fish that spend most of their growing season inshore and so are subject to greater stresses from the inshore estuarine environment. Unfortunately too few fish from the faster-growing population were collected to permit a comparison of metabolic responses between fish of the two growth regimes.

The difference in active and standard metabolic rates has been called "scope for activity", or most simply "scope" (Fry 1947). The difference between standard and routine metabolism has similarly been called routine scope (Beamish 1964a). Scope and routine scope are recognized as indicators of an organism's capacity for activity and are sensitive to changes in the acclimation temperature and season (Brett 1972). In the present study routine scope was measured by the difference between the calculated standard metabolism (extrapolated from the swimming speed-metabolism relation using Brett's 1964 method) and the metabolic rate at the *ad libitum* swimming speed. This corresponds to observed natural swimming speeds of migrating mullet and may be used in expressing the average metabolic rate of a fish in calculations of daily energy expenditures. "Routine" metabolism has commonly been used for this measure (Winberg 1956, Mann 1965, Healey 1972, MacKinnon 1973, Hoss 1974); however, this term by itself is ambiguous (Brett 1962) and so it would seem desirable to use metabolism determined at a realistic activity level (Small 1975). Brett (1962) and Brett and Sutherland (1965) have suggested using a swimming speed of one length per second as a uniform level for routine metabolism. This speed corresponds to the point where variability in oxygen consumption due to excitation becomes negligible. Webb (1975) has also incorporated moderate levels of swimming activity (routine swimming) into the defined limits of "routine metabolism". Such a procedure makes sense and should provide more uniform and realistic estimates of the average energy expenditure by moderately active fishes. In addition one length per second seems to be a preferred cruising speed in many species of moderately active fish (Wohlschlag *et al.* 1968) and approximates the swimming speed with the greatest hydrodynamic efficiency calculated by Weihs (1973). In most seasons the *ad libitum* swimming speeds observed in mullet are somewhat less than one length per second (see Table 1).

Figure 2 illustrates routine scope for both species in each season. For striped mullet scope levels off above 20 C while in the white mullet scope continues to increase up to the highest experimental temperatures. The greater expenditure of energy for swimming by the white mullet is apparent in these figures except

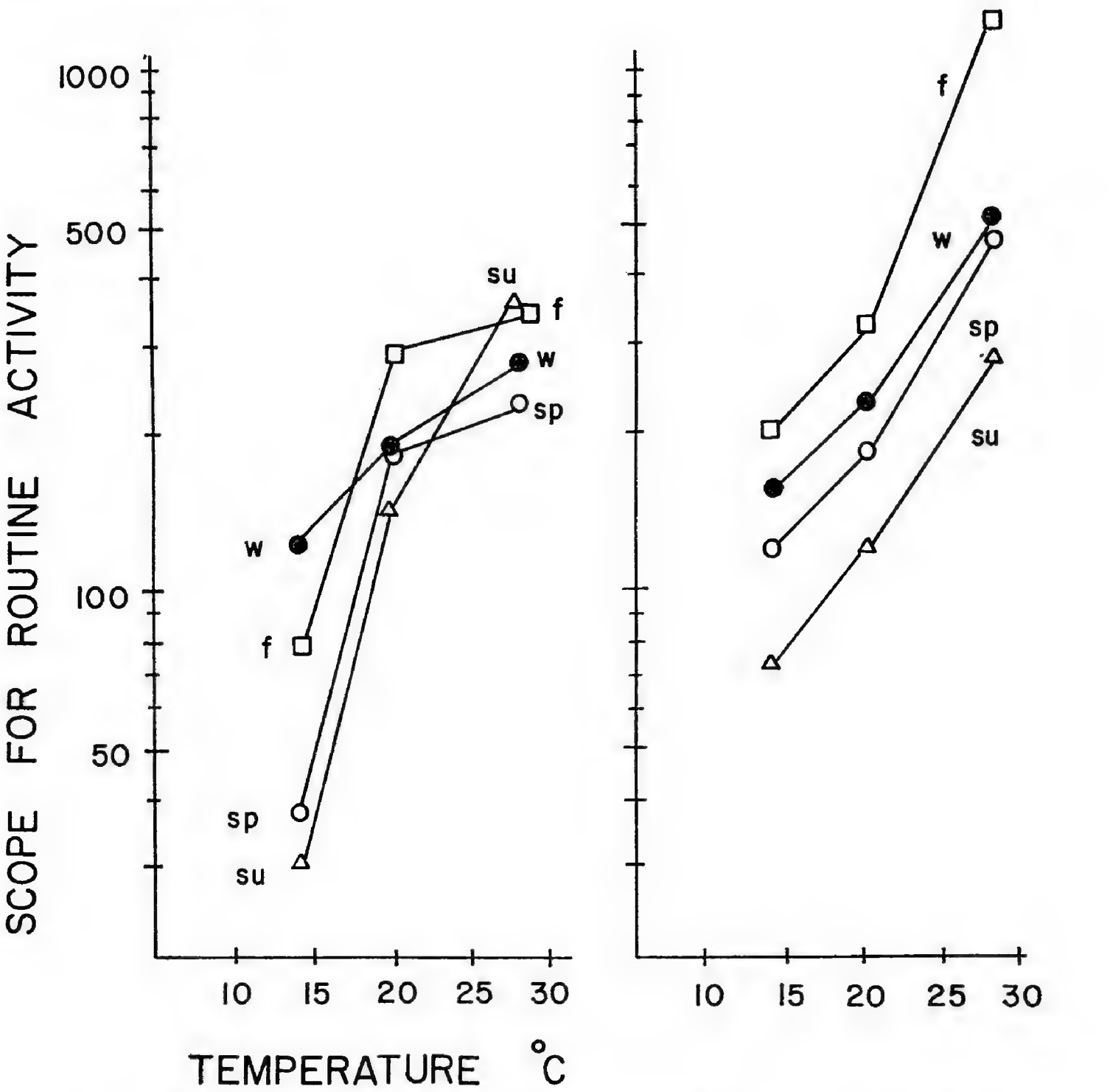

FIG. 2. The effect of season and temperature on Scope for Routine Activity in striped mullet (left figure) and white mullet (right figure). Scope expressed in units of mg O_2/kg/hr. Seasons abbreviated: w = winter; sp = spring; su = summer; f = fall.

at the ambient summer temperatures (25–30 C) when the warm-adapted species requires less energy to maintain its routine level of activity.

Effects of Seasonal Acclimatization Upon Respiration

Figure 2 illustrates the seasonal change in metabolism calculated at *ad libitum* swimming speeds for 140-gram fish at 20 C. Winter rates are higher than summer rates (see Table 4 and Table 5) for both species indicating that seasonal acclimatization like that found in other species (Wohlschlag and Juliano 1949, Beamish 1964b, Roberts 1964, Wohlschlag *et al.* 1968) is also found in both species of mullet. Discussions of possible mechanisms responsible for seasonal acclimati-

TABLE 4

Calculated respiration rates (mg O_2/hr) for average size (140 g) fish at 20 C

Species	Season	No. of fish	Standard	Routine (ad libitum) swimming	1 l/sec swimming
Mugil cephalus	winter	31	120	314	363
	spring	24	74	261	320
	summer	18	122	268	310
	fall	27	101	393	310
Mugil curema	winter	10	121	349	294
	spring	18	82	266	357
	summer	24	108	132	232
	fall	22	75	395	195

zation are given by Hoar (1959), Caldwell and Vernberg (1970), Somero and Hochachka (1971), and deVlaming (1972).

The ecological significance of seasonal acclimatization is that fish may maintain a more-or-less constant metabolic rate and hence a more constant level of activity throughout the year. Wohlschlag *et al.* (1968) found that the routine metabolism of the pinfish, *Lagodon rhomboides* varies only about 100 mg/kg/hr (average value 505 mg/kg/hr) over a 14 C annual temperature range. Mac-

TABLE 5

Comparison of regression intercepts

Comparison	DF	T	P	Outcome
Intercept "a" value, *cephalus-cephalus* comparisons				
W-SP	53	27.27	<0.01	reject
W-SU	47	27.62	<0.01	reject
W-F	56	3.79	<0.01	reject
SP-SU	40	—1.99	>0.05	accept
SP-F	49	—23.59	<0.01	reject
SU-F	43	—24.49	<0.01	reject
Intercept "a" value, *cephalus-curema* comparisons				
W-W	39	—3.10	<0.01	reject
SP-SP	40	—21.07	<0.01	reject
SU-SU	40	—26.47	<0.01	reject
F-F	47	34.47	<0.01	reject
Intercept "a" value, *curema-curema* comparisons				
W-SP	26	4.39	<0.01	reject
W-SU	32	5.62	<0.01	reject
W-F	30	30.84	<0.01	reject
SP-SU	40	0.46	>0.05	accept
SP-F	38	30.73	<0.01	reject
SU-F	44	35.63	<0.01	reject

W = winter; SP = spring; SU = summer; F = fall. Null hypothesis is that there are no differences.

Kinnon (1973) found virtually identical respiratory rates in American plaice, *Hippoglossoides platessoides*, during all seasons at ambient temperatures (1–6 C). Seasonal compensation in white and striped mullet is not as precise as for pinfish or plaice although, as shown in Figure 3, the difference in summer and winter metabolism is less than would be predicted.

Zoogeographical and Latitudinal Considerations

Physiological differences have been noted between zoogeographically distinct species of fish by several authors. The phenomenon of cold adaptation has been known for many years in polar fishes (Scholander *et al.* 1953; Wohlschlag 1960, 1964) but its existence has recently been questioned by Holeton (1973, 1974). Holeton's findings demonstrate the apparent lack of cold adaptation in several sedentary species (1974) which might otherwise be expected to have lower routine metabolic rates or in fish from a high arctic lake (1973) which has been shown to be "metabolically depressed" (Lasenby and Langford 1972, Rigler *et al.* 1974).

The bulk of the other experimental evidence indicates that latitudinal adaptation does occur in the metabolic rates of fishes. Barlow (1961) found species and habitat-specific differences in the rate of oxygen consumption when populations of two gobies *Gillichthys mirabilis* and *G. seta* were compared. Graham (1971) found lower respiratory rates in marine fish from the Caribbean Sea than in closely related species from the cooler Pacific Ocean when the two were tested at the same temperatures and he also found a positive correlation between the upper lethal temperature and habitat temperature for populations of *Abudefduf troschelli* from different latitudes (Graham 1972).

The lower rates of standard metabolism exhibited by white mullet (Table 3) may also be attributed to latitudinal adaptation. If cold adaptation exists, then the reverse phenomenon, warm adaptation must also exist, since one is simply relative to the other. Edwards *et al.* (1971) and Moore (1973a) have suggested possible reasons for, or advantages in, reduced metabolic rates in tropical areas. White mullet are found primarily in the tropics and their warm-adapted physiology is apparent from more than just the relative level of their metabolic rate. Their greater cold sensitivity and their greatest scope for activity at the highest temperatures are both other indications of warm adaptation. Striped mullet represent a warm-temperate species and possesses a physiology which reflects the species' warm-temperate, estuarine habitat. It appears to be more eurythermal in that it certainly tolerates lower temperatures than *M. curema* (Moore 1976), although it does not occur at as high temperatures as *M. curema* (Moore 1973b, 1974). In striped mullet the scope for activity levels off at temperatures above about 20 C. These data correspond with the observations by Liao *et al.* (1972) that striped mullet could not be induced to spawn at temperatures above 24 C. There is other evidence that the optimum temperature range for striped mullet must lie somewhere in the range of 20–24 C (Nash and Kuo 1975), a temperature range which corresponds to the local offshore temperature at the

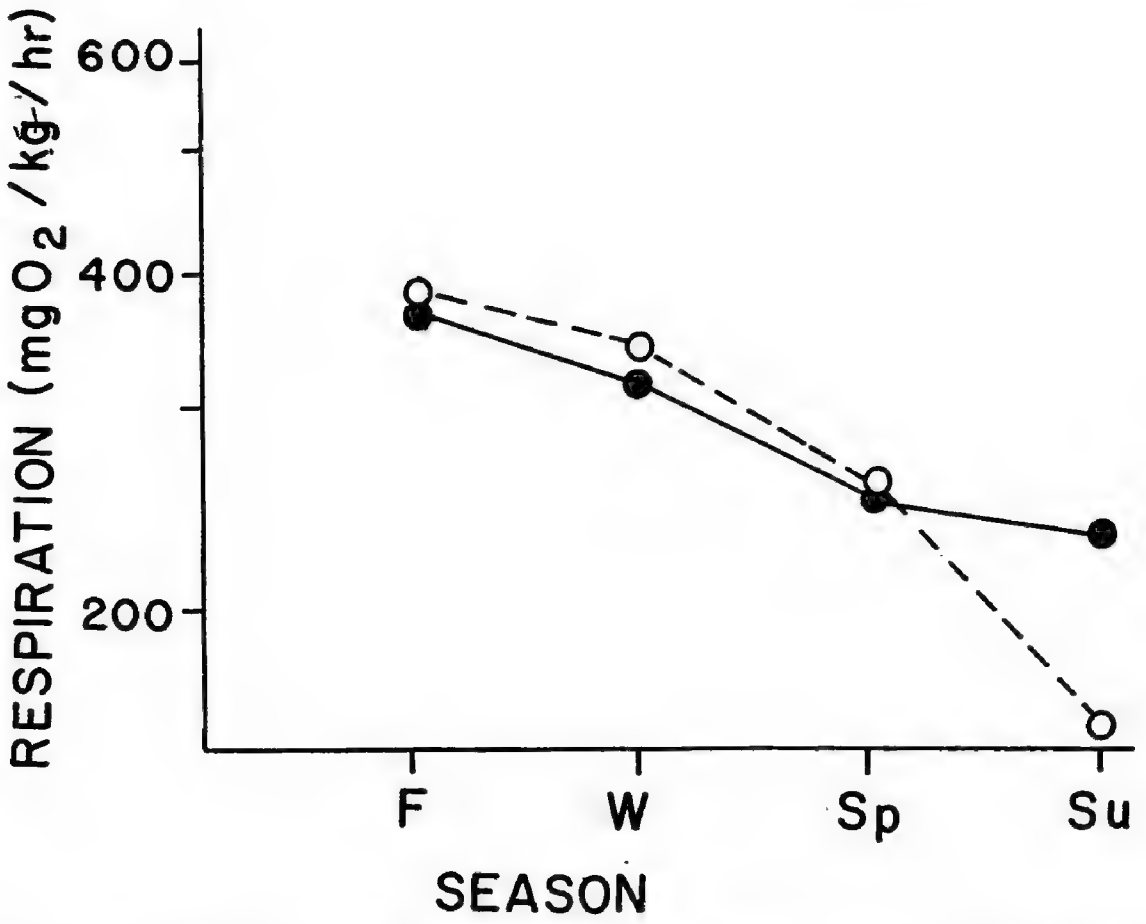

FIG. 3. Seasonal levels of oxygen consumption (mg O_2/kg/hr) calculated for a 140-gram fish at 20 C at the *ad libitum* swimming speed. Open circles = white mullet, closed cicles = striped mullet.

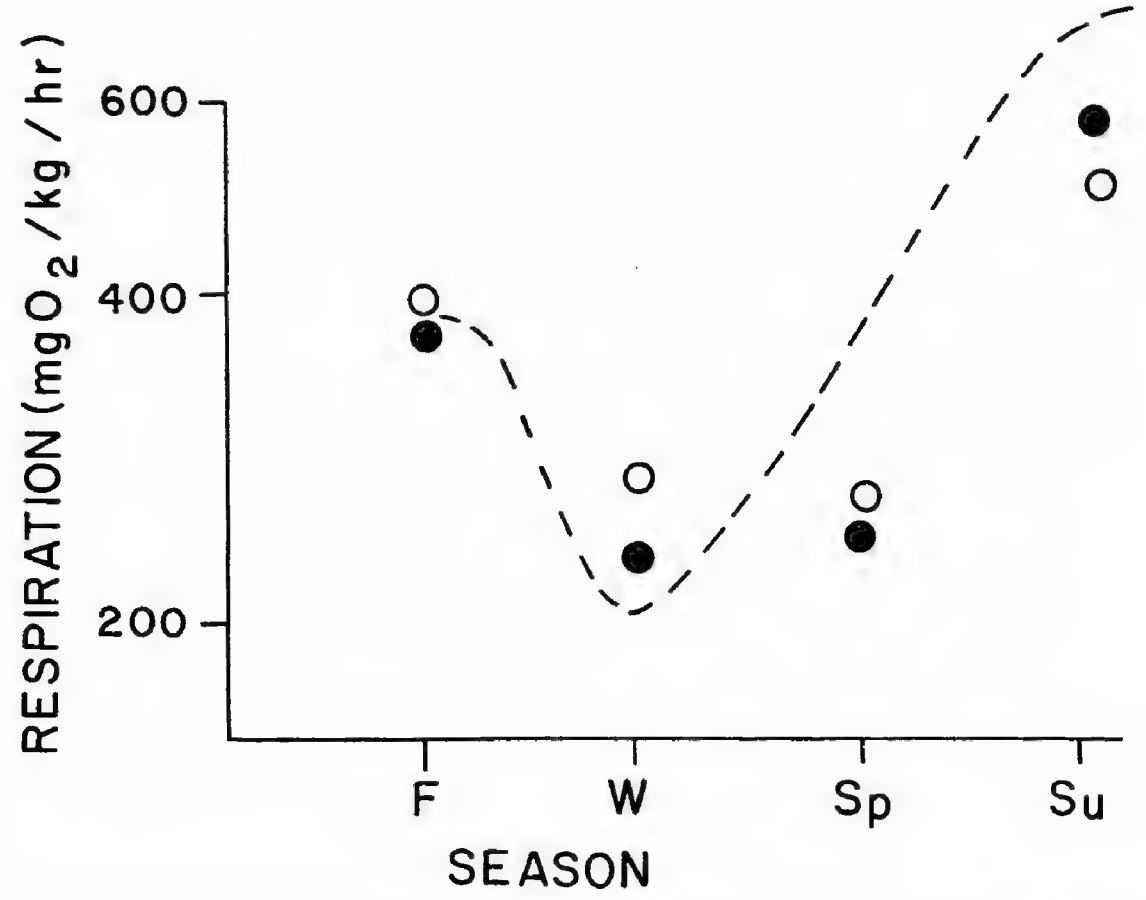

FIG. 4. Seasonal respiration at ambient temperature levels for striped mullet (closed circles) and white mullet (open circles) compared to a projected rate based on the average fall respiration rate and $Q_{10} = 2$. Ambient temperatures from Wohlschlag and Moore (ms): w = 14, sp = 20, su = 28, f = 22 C.

time of spawning but which exists in the inshore south Texas environment only a small part of the year.

ACKNOWLEDGMENTS

I wish to thank Dr. D. E. Wohlschlag for his continued support and encouragement during this study. Dr. J. J. Cech, F. Parker, and W. Longley assisted with much of the field work. Drs. David Farris and Don E. Hoss provided valuable criticisms to the manuscript. This paper is modified from part of a dissertation submitted to the Graduate School of the University of Texas in partial fulfillment of the requirements for the Ph.D. degree in Zoology. The manuscript was typed by Brenda Cox and Bonnie Laney.

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